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Meiosis in Milesia marginalis

S. M. Pady

(with plate 21)

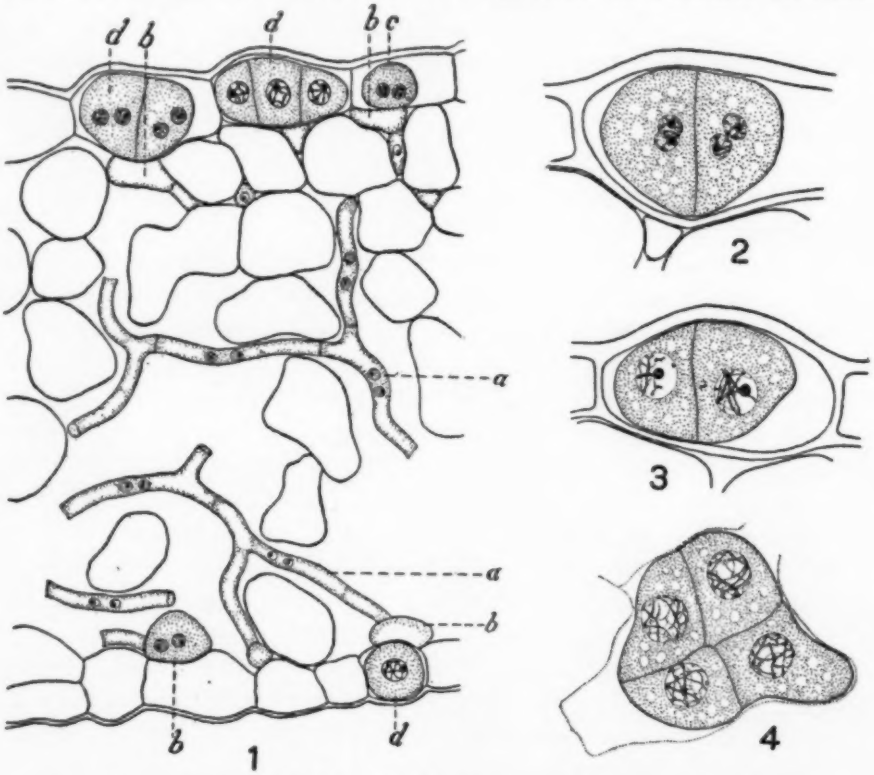
Nuclear division in the rusts has been the subject of study ever since the first nuclei were discovered by Schmitz in 1880, and valuable contributions have been made by Sappin-Trouffy, Blackman, Colley and many others. The rusts are rather favorable material for cytological study and present many and varied problems which are yet to be solved. I have recently reported on the two divisions of the fusion nucleus in the promycelium of *Hyalopsora aspidiotus* (Pady, *inedit.*), and shall give in this paper further data on the origin of the spindle, the details of prophase of the second division and the peculiar rod-and-ring division figure in the closely related species *Milesia marginalis*.

The teliospores of *M. marginalis* are formed in the spring in the epidermal cells of the old overwintered fronds of *Thelypteris marginalis*. The fronds usually die away as the season progresses but at the time the teliospores develop they are apparently still active. The development of the teliospores is indicated semi-diagrammatically in Text figure 1 which is a cross section through an overwintered frond. The mycelium, *a*, is composed of large hyphal cells, each with two prominent nuclei. Primordial cells, *b*, are formed just beneath both the upper and lower epidermis. The primordial cell penetrates the epidermal cell wall and its contents pass in to form the teliospore initial, *c*, which by growth and division becomes the multicellular teliospore, *d*. This type of development has been described in an earlier paper (Pady, 1933).

The two nuclei in the initial divide conjugately with the axes of their spindles parallel to the leaf surface. The daughter nuclei move apart and a cross wall is laid down, after which the nuclei take up a central position. This stage is well illustrated in text figure 2. Each nucleus has a well defined nucleolus and the chromatin appears to form a very coarse reticulum. When the young teliospore has reached its full size and nuclear division has been completed, the two nuclei in each cell come together and fuse. The nuclear membrane disappears at the point of contact and the two masses of chromatin merge. The two nucleoli remain distinct for a time, but later a single large nucleolus is present which presumably is the result of fusion, although the actual fusion has not been observed. The fusion nucleus rounds up and passes into a resting stage in which the chromatin is in the form of a very delicate but distinct network.

[The Bulletin for June (61: 279–343) was issued June 6, 1934]

The resting stage is of brief duration and the nucleus immediately enters into the heterotypic prophase. The chromatin comes to form a distinct spireme, and the nucleus increases tremendously in size. Text figure 3 is a cross section through a mature teliospore and shows clearly the two fusion nuclei. The chromatin is in the form of distinct threads which tend to lie around the periphery of the nucleus as is typical of diakinesis, with one or two strands connected with the nucleolus. In a surface view the



Figs. 1–4. *Milesia marginalis*. Fig. 1×920. Semi-diagrammatic drawing of a cross section of an infected frond illustrating the binucleate mycelium, *a*, in the mesophyll; the primordial cells, *b*, just below the epidermis; the initials, *c*, or young teliospores; the teliospores, *d*, in the upper and lower epidermis. Figs. 2–4×1540. Fig. 2. Young binucleate teliospore. Fig. 3. Later stage showing fusion nuclei. Fig. 4. Surface view of four-celled teliospore in upper epidermis.

nuclei are very prominent (text fig. 4), especially when stained with gentian-violet-iodine. The nuclei of the mature teliospore are thus not in the resting condition but have advanced into prophase. When germination takes place the fusion nucleus migrates out into the promycelium and immediately completes its division.

When viewed from above the teliospores display a wide variation in shape, size and number of cells, and in these respects indicate clearly the modifying influence of the epidermal cells. In text figure 5 a number of teliospores have been drawn to illustrate the great diversity that may be found. Where the epidermal cell is narrow and elongated the cells of the spore may be in a linear row (text fig. 5, A, C, D). On the other hand where spatial relations require it, the teliospore may become more compact or spherical (text fig. 5, G, H, I, J). All gradations between these two types may be found (text fig. 5, B, E, F, J). In any group of spores there are

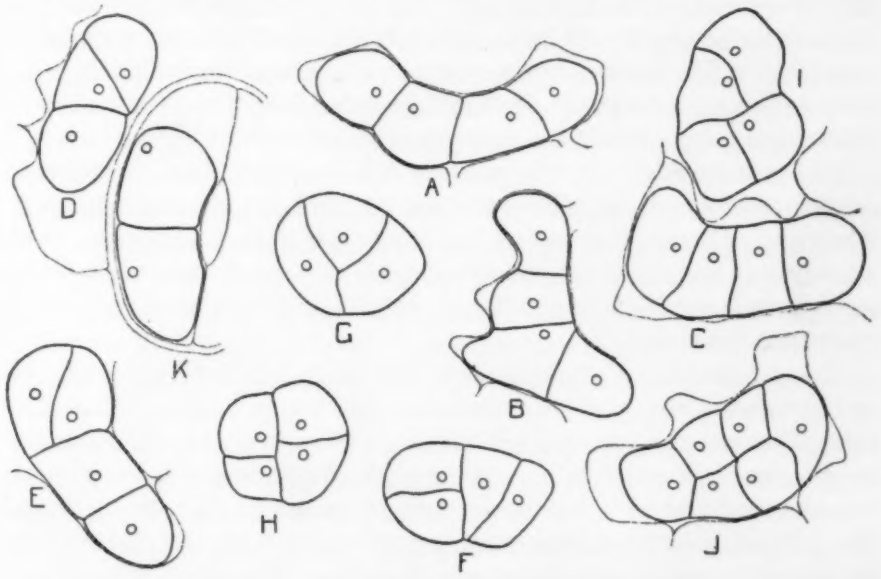


Fig. 5. *A–J*. Group of teliospores illustrating the variation in shape, size and number of cells and the modifying influence of the epidermal cells whose outline is shown by dotted lines. A single germ pore is found in each cell of the teliospore. ×1540.

many irregularities, as for example the two-celled spore in the guard cell of a stoma (text fig. 5, K). Each cell possesses a well marked germ pore and it is at this point that the promycelium arises when germination takes place.

In *Milesia* germination follows as soon as the teliospores mature, and upon fulfilment of the essential conditions. As in *Hyalopsora*, moisture is the primary requisite and germination begins when the moisture content of the air approaches the saturation point. The material for this study was gathered on June 17th at 10:30 A.M. in the Temagami Forest Reserve in Northern Ontario. The fronds were placed between sheets of moist news-

print and kept in a moist chamber. Twenty-four hours later the fronds were examined under the dissecting microscope and the greyish white bloom on the surface of the leaves indicated abundant germination. By carefully selecting material under the high power of the dissecting microscope one is fairly certain of obtaining the desired stages.

The first indication of germination is a small white spot which appears in the cell wall immediately above the germ pore of the teliospore. This is the beginning of penetration of the wall and the formation of an opening through which the contents will pass into the promycelium. The opening, when completely formed, is slightly narrower at the base than at the top. Apparently penetration is by chemical action, and there is no sign of a papilla as in *Hyalopsora*, where it appears to break the epidermis in an essentially mechanical way. It should be noted here that germination in *Hyalopsora* takes place in the very young fronds and the walls of the epidermal cells are relatively thin, while in *Milesia* germination occurs in old overwintered fronds and the epidermal cell walls are greatly thickened. The many cells of a single teliospore do not germinate simultaneously and considerable variation may be found. It is not uncommon to find two promycelia from neighboring cells one of which is in a much more advanced stage than the other.

The cell contents now commence to pass through the opening and push up through the surface of the frond as a small sac or vesicle, which elongates to become the promycelium. While the promycelium is still small the large fusion nucleus moves toward the point of exit. In one case a nucleus was observed just as it was commencing to move through the opening. The advancing portion in the opening was level with the leaf surface, and the chromatin was in irregular masses throughout the body of the nucleus. In *Hyalopsora* it was found that when the nucleus moved from the central part of the cell it lost its regular outline and stained very heavily, making it impossible to make out the details of its structure. As the nucleus of *Milesia* moves through the opening it becomes narrow and beaked and stains very heavily. Figure 1 (Pl. 21) shows an early stage. The nucleus becomes greatly attenuated and at one stage forms a dumbbell-like figure. Ultimately it slips through and remains for a time in the lower part of the young promycelium. At this stage the nucleus still tends to be quite irregular in shape and shows a strong affinity for the stain (Pl. 21, fig. 2). The cytoplasm remaining in the cell of the teliospore is markedly vacuolate (Pl. 21, fig. 1) but as the promycelium grows larger the entire contents move out leaving the empty cell wall behind.

The promycelia are easily dislodged and in the material studied were not readily found attached to the parent cell. This was undoubtedly due

to the necessity of repeated examination, although care was taken to reduce the amount of handling to a practical minimum. The rounded outline of many of the promycelia, together with the fact that the promycelium is independent of the teliospore in its subsequent development, seems to indicate that they may continue their normal development even when detached, provided that favorable conditions for development are maintained.

As the promycelium elongates the nucleus moves upward and assumes a more or less central position (Pl. 21, fig. 3). The nucleus is also at this stage usually somewhat irregular and stains very heavily, although the chromatin strands are sufficiently distinct to be recognized as late prophase. In the next stage the chromatin which is probably still in diakinesis, is more sharply defined and the nuclear membrane is distinctly rounded (Pl. 21, fig. 4). The nucleus now undergoes a marked change in appearance and the chromatin contracts into a heavily staining mass surrounded by a well defined hyaline area (Pl. 21, fig. 5). In the endosperm of *Iris*, Jungers (1931) found in late prophase that the nucleus contracted greatly and a perinuclear zone could be observed between the nuclear membrane and the cytoplasm. In figure 5 it is evident that no membrane surrounds the mass of chromatin and it is believed that it is represented by the rounded surface between the clear area and the cytoplasm. The spindle now begins to appear. The earliest stage I have found is shown in figure 6 in which the two poles of the spindle apparently coincide with the outer boundary of the clear area, suggesting very strongly the appearance of the intranuclear spindle, as found in the ascomycetes.

At each pole of the young spindle a small dark body is evident which is apparently a centrosome. From the poles the spindle fibres form a sharp V-shaped outline extending into the chromatin which stains very heavily. Although a sharply marked equatorial plate has not been observed, the chromosomes, which show up very clearly at this stage in *Hyalopsora*, are to be found at the centre of the spindle figure, and this stage undoubtedly corresponds to the equatorial plate stage. In figure 7 the chromosomes are beginning to move to the poles although individual chromosomes cannot be made out. This figure is very sharp and indicates the presence of a centrosome at each pole. The clear area around the spindle figure is less distinct in this figure, and in later stages it disappears entirely. Occasionally the chromosomes appear to move toward the poles in two distinct groups (Pl. 21, figs. 8, 9) but in general, anaphase is characterized by the spreading out of the chromosomes along the spindle figure (Pl. 21, figs. 10, 11). In figure 11 eight chromosomes may be counted. The chromosomes that have reached the poles begin to round up while the remainder are still

strung out along the spindle (Pl. 21, fig. 12). Telophase is characteristic with the two heavily staining somewhat irregular daughter nuclei at the poles, and the spindle fibres drawn into a single connecting strand (Pl. 21, fig. 13) which later disappears (Pl. 21, fig. 14). The presence of astral rays is indicated in the latter figure. They are very fine and delicate and the coarsely granular cytoplasm with its many small vacuoles makes their observation difficult.

During anaphase and telophase the division figure gradually elongates. This is clearly shown when figures 7 and 13 are compared. The young daughter nuclei also move toward opposite ends of the promycelia, and a nuclear membrane reorganizes about each one. A cross wall is formed and the promycelium becomes two-celled. The daughter nuclei immediately prepare for the second division, increasing greatly in size while the chromatin is in the form of a distinct reticulum (Pl. 21, fig. 15). As the nuclei enter prophase a well defined spireme is formed (Pl. 21, fig. 16), and a contraction phase similar to the one in the first division sets in (Pl. 21, fig. 17). The clear zone may appear on one side of the nucleus at first (Pl. 21, fig. 17) but it soon extends around the chromatin mass as contraction continues (Pl. 21, figs. 18, 19). In some cases a strand of chromatin may extend from the central mass through the clear area to the line bordering the cytoplasm (Pl. 21, fig. 19). This suggests that the nuclear membrane persists for a short time at least following the onset of contraction. In figure 20 two young spindle figures have been drawn, both taken from the same promycelium. At the tip of each pole is a minute but clear centrosome which appears to lie on the line previously occupied by the nuclear membrane. Similar spindles are shown in figure 21, only one pole of each spindle being visible. The spindle fibres extend into the central mass at a characteristic angle (Pl. 21, figs. 20, 21). In polar view their presence is indicated by a light area near the boundary of the heavily staining chromatin (Pl. 21, fig. 22).

It has not been possible thus far to demonstrate the origin of the two poles of the spindle. The evidence presented by the young spindles of both the first and the second divisions (figs. 6, 20) as to the existence of centrosomes at the poles of the spindles lying at the surface of the original nuclear membrane suggests that centrosomes are present on the nuclear membrane, and that they perhaps originate by division. Some of these figures are similar to those found by Olive (1908) in the multinucleate cells at the base of the aecium in *Puccinia Cirsii-lanceolati*, although they do not lend themselves readily to their interpretation as Hermann spindles.

In later stages the centrosomes at the poles are less distinct and the hyaline zone may persist for a time as in the first division (Pl. 21, fig. 23).

The spindle appears to elongate and the fibres form a rod-like structure (Pl. 21, figs. 24, 25). This may extend the length of the spindle to form a typical rod-and-ring type of division figure (Pl. 21, figs. 26, 27). These figures are similar in every way to those found in *Hyalopsora*. As anaphase begins the chromosomes move toward the poles (Pl. 21, fig. 28) and may become rather evenly distributed over the spindle (Pl. 21, fig. 29). The later stages are similar to those of the first division except that they are smaller (Pl. 21, figs. 30, 31). Occasionally promycelia are found in which division is more advanced in one cell than in the other, as shown in figure 32. In the upper cell is a typical telophase, while in the lower cell the spindle has practically disappeared and the young daughter nuclei are moving toward the opposite ends of the cell. This movement continues and the nuclei may come to rest against the median wall (Pl. 21, fig. 33). They are often pressed so tightly against the wall that they appear almost as a single nucleus. In the meantime the daughter nuclei have been gradually reorganizing and finally assume a spherical shape and a more median position in the cell (Pl. 21, fig. 34). A wall is formed and the promycelium becomes regularly four-celled. Each cell forms a sterigma (Pl. 21, fig. 35) and four basidiospores are formed as in other rusts.

DISCUSSION

In any group of promycelia there is a marked variation in size. Some promycelia are very small while others would be classed as "giants." In terms of volume their differences would be even greater. The explanation of this surprising variation, however, is not a difficult one. The teliospores of *M. marginalis*, as in related genera possessing intraepidermal teliospores, are extremely irregular. Cells of different teliospores and even cells of the same spore display differences in diameter and in volume. Since a single promycelium contains the entire contents of a teliospore cell, the variations in the size of the promycelia correspond to the variations found in the teliospores.

The two nuclear divisions in the promycelium of *M. marginalis* add considerably to our knowledge of division in the rusts and especially in the fern rusts. The details of prophase are similar to those described for *Hyalopsora* (Pady *inedit*) and agree in general with the accounts of Holden and Harper (1903), Blackman (1904), Colley (1918), Allen (1933) and others. The beginning of prophase in the teliospore is a characteristic feature of division in this rust. In rusts that germinate after a resting period, the fusion nucleus apparently overwinters in the resting condition. *Milesia* and *Hyalopsora* differ in that germination takes place without a protracted resting period, and the beginning of prophase in the spore is a device to

facilitate rapid germination. Moreover, development and germination take place early in the spring when the leaves of the alternate host, *Abies balsamea*, are in a susceptible condition. A peculiar anomaly is found in *M. fructuosa* which forms teliospores at the end of the current season. In one fixation made on September 15th the teliospores were mature and the fusion nuclei were all in advanced prophase. Subsequent development was not followed, but if germination follows, it takes place at a time when the alternate host is not susceptible. On the other hand it is hardly likely that these thin-walled spores would survive the long and severe winter of the region in which they were collected. Since there is the possibility that this species may be a variant of *M. intermedia*, further culture studies are desirable.

One of the peculiar features of late prophase in *Hyalopsora* was the tremendous reduction in volume of the fusion nucleus with the chromosomes formed inside what was called the nuclear membrane. In the light of the well marked contraction phase in *Milesia*, the presence of a contraction phase in *Hyalopsora* is strongly suggested. According to this view the so-called nucleus is not a true nucleus but is simply the contracted chromatic material in the late prophase or the equatorial plate stage. Minute centrosomes are found at the poles of the young spindle but their presence has not been demonstrated in later stages or in resting nuclei. These centrosomes are located on the nuclear membrane and when contraction begins, followed by disappearance of the nuclear membrane, they retain their position as indicated clearly when the spindle fibres begin to form.

At first the young spindle is entirely contained in the area of the original nucleus, so that in one sense it is intranuclear. Later, however, the spindle elongates greatly and the outline of the nucleus, which is represented by a clear area surrounding the group of chromosomes, gradually disappears. Olive (1908) found that nuclear division was intranuclear and the spindle as it elongated stretched the membrane considerably. Olive was able to differentiate between a Hermann "centralspindel" and mantle fibres. In *Milesia* such a distinction cannot be clearly drawn.

At this stage in both *Milesia* and *Hyalopsora* the spindle fibres form a cylindrical "rod" which, passing through the dense chromatin mass, gives the characteristic rod-and-ring appearance. The spindle fibres tend to retain the stain as Bělar (1926) found in the "achromatic cones" of the division figures in *Aggregata eberthi*, and thus accentuate this appearance. This type of division figure is prominent in the second division of the two fern rusts that have been studied and is probably characteristic of these so-called primitive rusts. *Milesia marginalis* and *Hyalopsora aspidiotus* are both long-cycled heteroecious rusts and exhibit none of the tendencies to-

ward reductions in their life-cycle, as for example, in *Puccinia Podophylli* (Jackson, 1931), or in their nuclear history, as in the various cytological races of the short-cycled rust, *Caeoma nitens* (Dodge, 1924). This would be expected when it is remembered that the rusts have evolved along with their hosts (Jackson, 1931), and thus these fern rusts in their evolutionary history have become fixed in their life cycle and in their nuclear history.

SUMMARY

1. The fusion nucleus in the teliospore, following a brief resting stage, enters into prophase forming a well defined spireme.

2. Germination is immediate and the nucleus enters the promycelium in late prophase.

3. A contraction phase is present in both divisions, the chromosomes contracting into a dense mass inside the nuclear membrane which gradually disappears.

4. The young spindle ends in centrosomes located in the region previously occupied by the nuclear membrane.

5. The chromosomes are more or less massed on the spindle and move to the poles in irregular masses.

6. A spireme is formed in the prophase of the second division.

7. Rod-and-ring division figures similar to those found in *Hyalopsora* are characteristic of the second division and it is believed that they represent the equatorial plate stage.

The writer wishes to acknowledge the assistance of Dr. B. O. Dodge and Dr. R. A. Harper in examining the preparations and reading and criticizing the manuscript. This work was completed during the tenure of a National Research Council Fellowship.

The New York Botanical Garden

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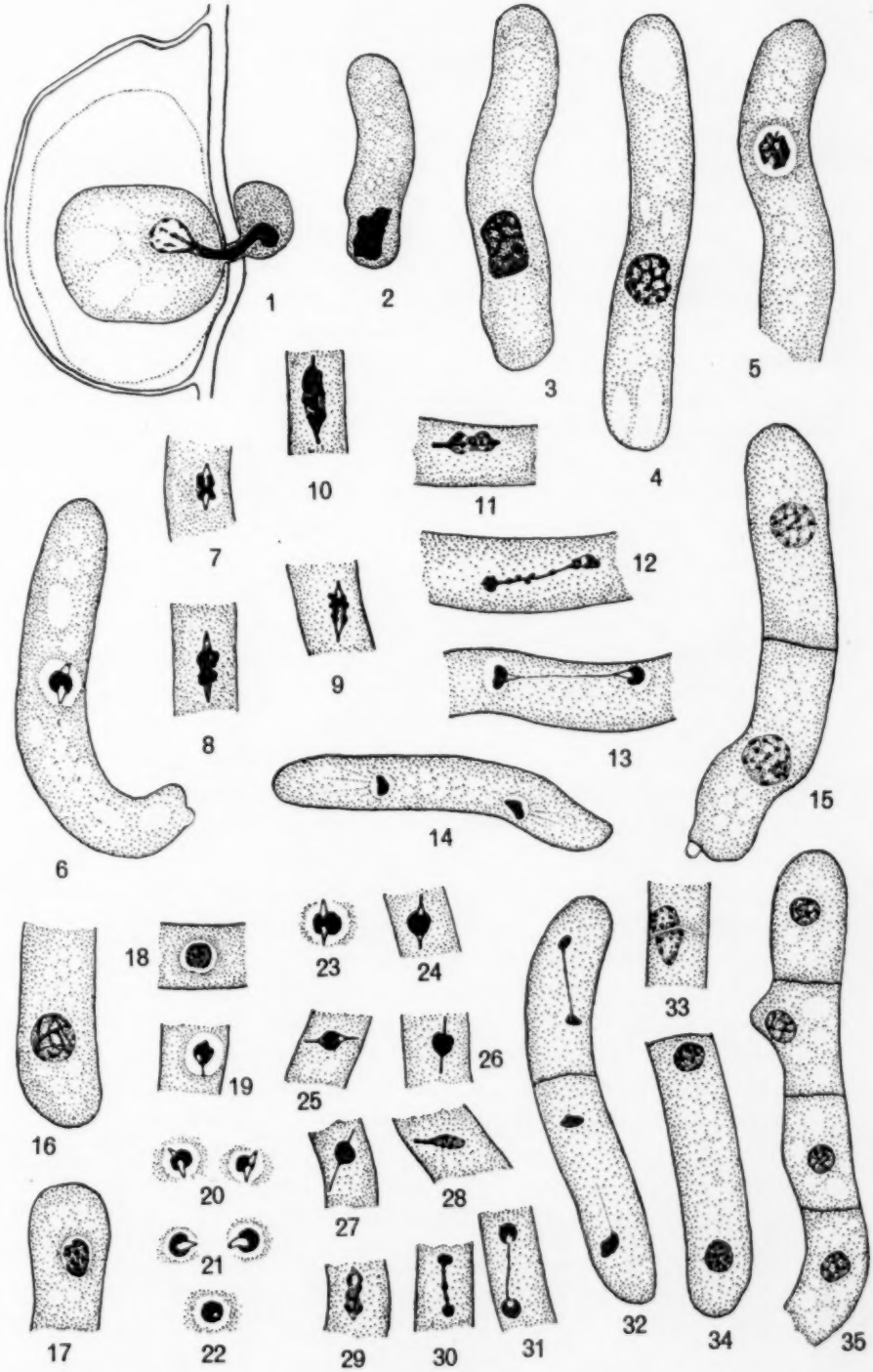
———— *inedit.* A cytological study of the development and germination of the teliospores of *Hyalopsora aspidiotus* (Pk.) Magn.

Explanation of plate 21

All figures ×1540

Milesia marginalis

Fig. 1. Passage of nucleus into promycelium.
Figs. 2–4. Late prophase.
Fig. 5. Contraction phase.
Fig. 6. Young spindle.
Figs. 7–12. Anaphase.
Figs. 13–14. Telophase.
Fig. 15. Two-celled stage.
Fig. 16. Prophase of second division.
Figs. 17–19. Contraction phase of second division.
Figs. 20–23. Young spindles.
Figs. 24–25. Later stages.
Figs. 26–27. Typical rod-and-ring division figures.
Figs. 28–30. Anaphase.
Figs. 31–32. Telophase.
Fig. 33. Nuclei crowded against median wall.
Fig. 34. Daughter nuclei completely reorganized.
Fig. 35. Four-celled stage, two cells forming sterigmata.



PADY: MILESIA

The Origin of the foliar pseudo-bulbils in Kalanchoë daigremontiana

MARION A. JOHNSON

(WITH THREE TEXT FIGURES AND PLATE 22)

Bryophyllum has long been used by botanists as the classical example of a plant illustrating regeneration from detached leaves. Recent studies by Howe (1931), Naylor (1932), Yarbrough (1932) and Freeland (1933), have conclusively demonstrated that the plantlets in question may be produced, or are at least initiated, in the normal ontogeny of the leaf before removal and have thus cast serious doubt upon the advisability of regarding this phenomenon in *Bryophyllum* as regeneration. In this connection the writer wishes to call attention to *Kalanchoë daigremontiana* R. Hamet et Perrier de la Bâthie, which is far more prodigal in the production of foliar plantlets or pseudo-bulbils than is *Bryophyllum*.[1] Under good growing conditions a single plant may give rise to several hundred pseudo-bulbils; it is not uncommon for a large leaf to bear as many as sixty in various stages of maturity (figs. 1 and 2) while flowering specimens may produce a large number in the axils of bracts on the inflorescence axis.

Kalanchoë daigremontiana is native to Madagascar but has been widely introduced into the United States so that it may be readily obtained from growers of succulents. Greenhouse culture is similar to that for *Bryophyllum*.

The habit of the plant resembles *Bryophyllum* in that it is relatively unbranched and about six decimeters in height although flowering specimens may measure two meters. The succulent leaves are opposite and decussate. The blade is broadly lanceolate with serrate edge and peltate base. The basal leaves are abscissed until at the conclusion of the flowering period the plants are leafless. The inflorescence is a cyme bearing a profusion of pendulous, pink flowers, 2.5 cm. in length.

The pseudo-bulbils are produced freely in summer but are suppressed during December, January and February, except in the inflorescence. In March, however, when the days are appreciably longer they begin to appear once more on the leaves. They may also be induced at any time during the year from severed leaves either by placing them in moist chambers or by standing the petioles in water.

At the time of dispersal the pseudo-bulbils generally have six leaves. The first pair, somewhat unequal in size, are thick, sessile, and orbicular

[1] The ease with which *Kalanchoë daigremontiana* may be propagated by pseudo-bulbils has recently been noted by Swingle, C. F. 1933. The easiest plant in the world to propagate. Jour. of Heredity, **25**: 73–74.

in shape with a broadly obtuse tip and entire edge. The second pair are broadly elliptical, with obtuse tip, entire edge and with the base tapering into a short petiole. The third pair is similar to the second except that the blade is more elliptical in shape and has two to four deep serrations on each edge. The base of the pseudo-bulbil is much swollen immediately above the attachment to the parent leaf. Roots arise from this region as well as from both the nodes and internodes and may make their appearance before the plantlets are detached.

Figs. 1 and 2. Fig. 1. Photograph of leaf from lower surface showing pseudo-bulbils; $\times\frac{1}{2}$. Fig. 2, lower surface of leaf showing pseudo-bulbils bearing plantlets of a second order; $\times 1$. Both leaves were in condition shown when removed from plant for photographing.

The material for this study was taken from leaves of well grown plants. The terms pseudo-bulbil and plantlet have been used interchangeably although it is recognized that technically pseudo-bulbil may be considered the more appropriate because of the enlarged, bulb-like base. On the other hand, the term plantlet may be equally well employed since roots, stem and leaves are organized before dispersal.

DEVELOPMENT OF THE LEAF

In order to determine the ultimate origin of the pseudo-bulbils it was necessary to work out the ontogeny of the leaf. The following brief outline is presented to clear up those points having a bearing upon the problem. The primordia appear decussately as broad, round-topped cones of meristematic tissue from the stem tip. When an approximate height of 90μ is reached, the conical alignment is displaced by considerable enlargement of the cells in the basal portion of the abaxial faces so that the primordia curve inward until they completely overarch the apex of the stem.

Cell division is quite general throughout the primordia at this stage, three chief centers of activity can, however, be recognized: the first is at the tip and is responsible for apical growth which persists for a short time; the second is in the region of the midrib and contributes to that part of the blade and petiole; while the third is located in the adaxial face and gives rise to the lamina.

Apical growth ceases when the primordia are about 0.9 mm. in length. Meristematic activity is now transferred from the distal end to the base in the form of two ridges of tissue extending along the edges of the adaxial face. These curve inward until they meet, thereby forming an arc of tissue which is responsible for the turned up edge of the peltate base seen in adult leaves.

Transverse sections through young leaves show eleven layers of cells (fig. 4). The nine inner ones give rise to the mesophyll and can be traced to the activity of a single sub-epidermal cell at the edge of the leaf. This cell is but one of a row extending throughout each ridge of the developing lamina. These mesophyll mother cells, as they may be designated, maintain their position according to the scheme described for the tobacco leaf by Avery (1933). The mother cell divides at right angles to the upper surface of the leaf, then the outer cell divides parallel to the leaf surface forming the two cells *a* and *b* seen in fig. 4. One of these, say the upper *a*, becomes the initial which divides as the original mother cell until three cells equivalent to the ones just described are formed; but now, it is the lower instead of the upper cell from this new series which becomes the initial. Thus it can be seen that the position of the row of mesophyll mother cells remains relatively unchanged throughout the development of the leaf. The young lamina is built up with an entire edge until a length of about .9 mm. is reached, when slight undulations make their appearance. These are predetermined by a difference in the rate of division which exists in certain portions of the row of mesophyll initials and its derivatives. Ultimately all the cells in the active centers mature forming conspicuous serrations, while

the initials at the base of the notches remain meristematic. Cell division here is retarded although not completely suspended, as is evidenced by the occurrence of occasional mitotic figures.

The structure of the mature leaf is extremely simple, there being no differentiation into palisade and spongy mesophyll. All of the cells except those in the epidermis are well supplied with chloroplasts. Mature leaves, exclusive of the midrib, are from 15 to 20 cells in thickness. A bluish-red pigment which has been identified as anthocyan is found in the second layer of cells within the epidermis (*c*, fig. 4), as well as in localized areas throughout the leaves.

ORIGIN AND DEVELOPMENT OF THE PSEUDO-BULBILS

The production of the pseudo-bulbils is intimately associated with the origin of the notches between the serrations and in time of development parallels the growth of the leaf. The inhibitory action of rapidly growing plantlets on the growth from other notches as described by Loeb (1924) for *Bryophyllum calycinum* Salisb. could not be detected in attached leaves. As has been noted maturation of the leaf begins first at the distal end and progresses basipetally in an orderly sequence, thus the oldest plantlets are found at the tip with a graduated series of younger ones extending down into the notches of the peltate base. All stages in development may be had in leaves between five and twenty centimeters in length.

The youngest leaves in which the origin of the pseudo-bulbils could be traced were from 2.5 mm. to 3 mm. in length. Figure 5 was drawn from a section taken through the bottom of a notch from such a leaf and when compared with figure 4, which represents a comparable view before a new plantlet has been initiated, indicates the extent to which development has taken place. It is to be noted that the row of mesophyll initials can no longer be distinguished. In their stead six rows of subepidermal cells (seen between *a* and *b* in fig. 5) two tiers in depth extend along the bottom of the shallow notch so that the edge is considerably thickened. These cells are smaller than those from a similar position in younger leaves and continue further around the edge (between *b* and *c* in fig. 5). Serial sections through older notches show that the six rows of cells just described initiate the formation of a very active meristem which is oval in shape, 84μ in length by 68μ in width and 4 to 5 cells in depth with a convex outer surface covered by a thick cuticle (figs. 6 and 8). This meristem becomes more massive until its free face measures some 112μ by 109μ when two leaf primordia originate in the same manner as from the stem tip of an older plant except that one can be recognized slightly earlier and is the larger of the two (fig. 10). The less active cells in the slight concavity between the primordia

represent the stem tip. A prominent provascular strand soon differentiates from the base of each primordium until it connects with the veins entering the notch.

Coincident with the organization of the plantlet meristem the cells seen in the region between *b* and *c* in figure 4 become active and extend the bottom of the notch over the edge of the leaf as a trough with the tip curved upward (figs. 6, 7 and 13). For want of a better name the writer has designated this projection as the "peg." It matures at the tip and is then built out from the base so that the plantlet is carried out of the notch. At maturity the peg is 3 to 4 mm. in length and is inclined from 60°–120° to the plane of the blade.

The pronounced swelling at the base of the first pair of leaves where attachment to the peg is made appears early and in figure 10 is seen as a slight protuberance on the right of the large primordium. It is formed by the ultimate enlargement and change in orientation of the cells in this region and not by an appreciable increase in cell division as might be expected. Plantlets about .5 mm. in height show that approximately seven rows of cells in the outer part of the base are involved. At first these cells are uniform in size and arranged vertically, however, as growth progresses some six or eight cells from each row commence to enlarge almost at right angles to the leaf primordium while those slightly lower in the same rows elongate parallel to the same axis. The result of this unequal growth is a large swelling with a sharp constriction where attachment is made to the peg (figs. 3, 12 and 14). The cells in the attachment are somewhat bent back on themselves and appear to be under stress, perhaps due to tension set up by the cells in the swollen region above. The enlarged base of the pseudo-bulbils which may measure 1–2 mm. in diameter, at time of shedding, serves a threefold function: first as a storage organ; second as a point of origin for the first roots; and third as a unique organ for detaching the plantlets from the peg.

The storage function is first manifest in the peg, where the parenchyma becomes filled with large starch grains. This reserve food supply gradually diminishes as the tissues of the pseudo-bulbil mature and the cells in the swollen base and thickened leaves soon contain an abundance of starch which is confined to the peripheral layer of the cytoplasm. The prominent central vacuole serves as a reservoir for water, thus the young plantlet is provided with a food and water supply until it can establish itself. A well developed cuticle aids in reducing transpiration.

The appearance of the root is late in comparison to that of the stem and leaf primordia; pseudo-bulbils with the first pair of leaves 3–4 mm. in length show nothing which can be interpreted as root development (fig.

14). The writer's observations thus far do not include the exact stage at which the roots are initiated, but plantlets with two pairs of leaves have well organized roots as are to be seen in figure 3. Each large root is accompanied by two lateral ones, so that they occur in groups of three on a broad base of meristematic tissue which is intimately associated with the vascular system. Roots may be produced from both the nodes and the internodes as well as the swollen base of the plantlets.

The problem of pseudo-bulbil detachment has proven to be of considerable interest. The presence of dozens of plantlets under well grown specimens in the greenhouse would suggest that they might be cut off by abscission layers as is common in deciduous leaves. Examination of the

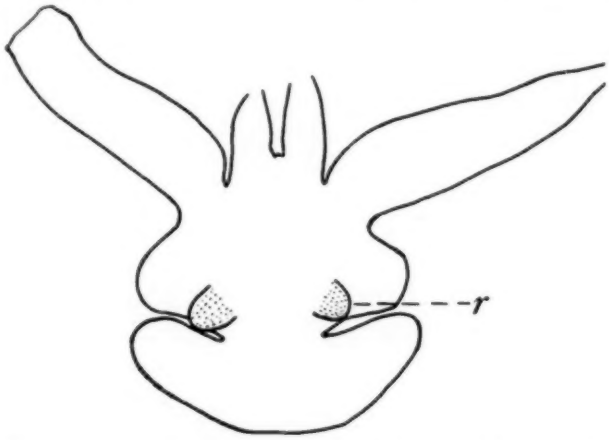


Fig. 3. Transverse section through peg showing: attachment of pseudo-bulbil; swollen base which serves as a fulcrum in detaching plantlet; *r*, root; ×24.

attachment region fails to show any sign of an abscission layer. Cytologically the cells have every appearance of being in good living condition. They are distended by a large central vacuole, have thin walls without visible signs of disintegration and resemble the other living cells except in being free from starch. Evidence to support the usual explanation of abscission is lacking. A study of sections as represented in figure 3 suggests that pressure brought against the peg by the developing roots might break the attachment; while this may be a contributing factor, yet roots often appear while the plantlets are still attached to the parent leaf without freeing them (fig. 2). The method of detachment appears, in final analysis, to be mechanical and is interpreted as follows. In figures 1 and 14 it will be seen that the pseudo-bulbils are offset by the peg so that they are not protected by the edge of the leaf, and therefore may be readily struck by raindrops or brushed by swaying leaves. Furthermore the plantlet appears to

have been girdled by an invisible band which has almost effected separation from the peg (fig. 3). The attachment is small in comparison with the swollen base of the plantlet although it is traversed by two or more vascular bundles. It is to be further noted that the enlarged base is asymmetrical with the outer face the more highly developed. A comparison of the plantlet to a lever of the first kind attached at one end near which there is a fulcrum is especially enlightening. The connection between plantlet and peg represents the attachment of the lever, while the stem axis and leaves comprises the lever itself and the projecting edge of the asymmetrical base is in contact with the peg which serves as the all-important fulcrum. It can readily be seen that sufficient force applied to the lever will detach the whole system. This is to be expected since the vascular bundles of the slender attachment are small and the remaining cells are thin-walled and distended by turgor pressure in addition to being under tension, all of which contributes to the ease with which they may be severed by lateral stress. The efficiency of this mechanism is easily demonstrated, a slight touch on the thick stiff leaves of the pseudo-bulbil frees it at once while greater force is required when applied at right angles to the peg in pulling off the plantlet. In undisturbed specimens plantlets of the first order remain attached to the parent leaf until they in turn bear pseudo-bulbils of a second order, which certainly is proof that an abscission layer has not interrupted the vascular supply (fig. 2). Furthermore, in the greenhouse withered leaves are frequently found on old plants with a number of the plantlets still attached which are finally shed with the old leaves. There is little doubt but that rain and wind are sufficient to detach the plantlets in nature. The importance of rain as a disseminating agent is further suggested by the fact that in the native habitat pseudo-bulbil formation is initiated during the rainy season. The nicety with which such a system functions in vegetative reproduction is readily appreciated for plantlets are not likely to be detached until they are large enough to offer resistance to mechanical force and by that time they are stored with starch and water and have leaves, stem and roots well organized.

DISCUSSION

The origin and organization of the meristems from which the pseudo-bulbils in *Kalanchoë daigremontiana* are produced compare favorably with that reported for the development of the foliar embryos of *Bryophyllum calycinum*. In both cases the development is directly associated with the normal ontogeny of the leaf and can be detected when the leaves are from two to four millimeters in length. This activity in *K. daigremontiana* is

initiated in the row of mesophyll mother cells located in the bottom of the young leaf notches. The same condition exists in *Bryophyllum calycinum* judging from the drawings of Naylor (1932) and Yarbrough (1932). The chief difference between the two is in the time of root development which is considerably later in *Kalanchoë daigremontiana*. In the plantlets observed no sign of a root meristem was found until after the first pair of leaves were partially developed.

Two species of *Kalanchoë*, *K. daigremontiana* and *K. tubiflora*, so far as the writer is aware, are unique among plants in having their pseudo-bulbils seated upon a peg from which they are readily detached by mechanical means. Advantageous as the peg may be for dispersal, it is not always developed, for example in the former species it is absent from the plantlets formed in the inflorescence. It is to be noted that here the plantlets are more exposed to the action of wind and rain which may free them more readily than from the leaf. This, however, is not being advanced as a factor in suppressing the peg. The swollen base is developed as in the foliar plantlets. Dispersal in this case may be delayed until the death of the parent plant which under greenhouse conditions appears to occur soon after flowering. When severed leaves are placed on moist soil, the plantlets produced root freely, but again, the peg is poorly if at all developed. In this instance there is no method for dispersal except through the decay of the parent leaf and subsequent washing by water as is reported by Ridley (1930) for *Bryophyllum calycinum*.

The detachment of the pseudo-bulbils by mechanical means as seen in *Kalanchoë daigremontiana* appears to be similar to that in *Cystopteris bulbifera* (L.) Bernh., *Lycopodium Selago* L., and *L. lucidulum* Michx. The propagules in these instances are supplied either with a swollen base or thick sessile leaves and a fragile attachment which is easily pried loose. In the case of *L. lucidulum* Smith (1920) reports that the bulbils are freed in part by a disorganization of the xylem walls in the attachment. Nothing resembling stages in decomposition of cell wall or cell contents could be found in *K. daigremontiana*. Smith (1920) further describes the accumulation of starch in *L. lucidulum* as being due to the absence of phloem in the constricted attachment. This raises the question as to whether the food stored in the pseudo-bulbil was produced by the parent leaf or the leaves of the pseudo-bulbil itself. The first evidence of stored starch is to be found in the peg and could have come only from the parent leaf since the pseudo-bulbil is still embryonic. Later this store of starch is gradually depleted and when the plantlet has developed its first pair of leaves, starch appears in the swollen base. The differentiation in the vascular bundles of the attachment is not sufficient to detect the presence of phloem with

certainty so that the reserve starch for the young plantlet may have come from either the parent leaf, from its own leaves or perhaps from both.

The view held by Kupfer (1907), Yarbrough (1932), and others, that growth from preformed meristems is not to be included under the phenomenon of regeneration is supported and strengthened by the writer's observations on the production of foliar pseudo-bulbils in *Kalanchoë daigremontiana*. It is to be noted that in summer these plantlets are not only initiated but are developed without a period of dormancy. They appear so early in the ontogeny of the leaf that they may be seen with the unaided eye long before the leaf has reached maturity. Furthermore they are not organized from mature cells which have been regenerated or rejuvenated but from cells which have never lost their meristematic qualities. It is clear then, that the formation of these plantlets represents a phase of growth intimately associated with the development of the leaf and which results in an efficient means of vegetative reproduction. The cessation of growth in the plantlet meristems during the winter months brings about a condition similar to that generally seen in the foliar embryos in *Bryophyllum calycinum* under greenhouse conditions. According to the observations of Ridley (1930) this species when growing in Jamaica bears bulbils on its leaves in abundance. If these observations by Ridley or the abundant production of pseudo-bulbils in *K. daigremontiana* had been available to Loeb (1924) it is doubtful whether he would have advanced his explanations for the activation of the foliar meristems in *Bryophyllum calycinum*.

The problem of inducing and breaking dormancy in plants may well be attacked in *Kalanchoë daigremontiana* which is more favorable for this type of experimental work than *Bryophyllum calycinum* upon which recent studies have been made. A distinct advantage over *Bryophyllum* is that plantlets are produced in abundance during the summer under good growing conditions but their growth is retarded throughout the winter so that dormant meristems are to be found in the leaf notches. These, however, become active upon the return of summer and grow out into plantlets. Experimental results obtained by varying the length of day, quality of light, humidity, amount of water, etc., either during summer or winter could be easily measured against the controls which according to the writer's experience have a definite, clear-cut behavior depending upon the season. Since plantlet formation is restricted to the time of year having long days it may well be that length of day is a factor in inducing or breaking dormancy of the foliar meristems. Experiments in support of this supposition have not been attempted. The failure of *Bryophyllum* to produce plantlets freely with the leaves attached may in part account for the negative results obtained by Freeland (1933) upon varying the length of day,

humidity and water supply for young plants. *Kalanchoë daigremontiana* is also suitable for studies in the activation of the dormant foliar meristems on severed leaves. Furthermore, the mechanism for detaching the plantlets is ideal for obtaining more accurate data on the mass relation of regeneration as demonstrated by Loeb (1924) for *Bryophyllum calycinum* leaves.

SUMMARY

1. A noteworthy feature in the life-cycle of *Kalanchoë daigremontiana* is the production of pseudo-bulbilis in the leaf notches of attached leaves. The degree of development attained is dependent upon the season. During the summer the pseudo-bulbils are matured and detached from the parent leaf while in winter they remain dormant as embryonic tissue in the leaf notches. Dormancy may be broken, however, by severing the leaves and placing them under suitable growing conditions. This treatment yields vigorous plantlets in a short time.

2. The ontogeny of the leaf is described briefly.

3. The origin of the pseudo-bulbils is determined. They are developed from the row of lamina mother-cells in the bottom of the leaf notches during the ontogeny of the leaf. The earliest stages are found in leaves 2.5 to 3 millimeters in length. Evidence is presented which indicates that the production of the pseudo-bulbils is not to be regarded as the result of regeneration.

4. The pseudo-bulbils are seated upon a grooved peg which is developed from the bottom of the leaf notches. This appears to be an unique organ in plants.

5. The pseudo-bulbils are provided with a swollen base which serves as a storage organ for water and food materials. It also acts as a fulcrum against which force supplied by wind, raindrops, etc., pries the plantlets from the peg. An abscission layer is not formed.

6. It is suggested the *Kalanchoë daigremontiana* would be a suitable plant for physiological studies in inducing and breaking dormancy.

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Explanation of plate 22

Fig. 4. Transverse section through young leaf showing: mesophyll mother-cell which has recently divided forming the two cells *a* and *b*; *c*, layer of cells containing anthocyan; ×365.

Fig. 5. Transverse section of leaf cut through notch showing: early stage in organization of pseudo-bulbil meristem from cells opposite *a*, these cells are derivatives from several mesophyll mother-cells similar to that in fig. 5; the cells in region between *b* and *c* which develop the peg; ×365.

Figs. 6 and 8. Transverse sections through leaves showing continuation of growth initiated in fig. 5; *p*, peg; ×365.

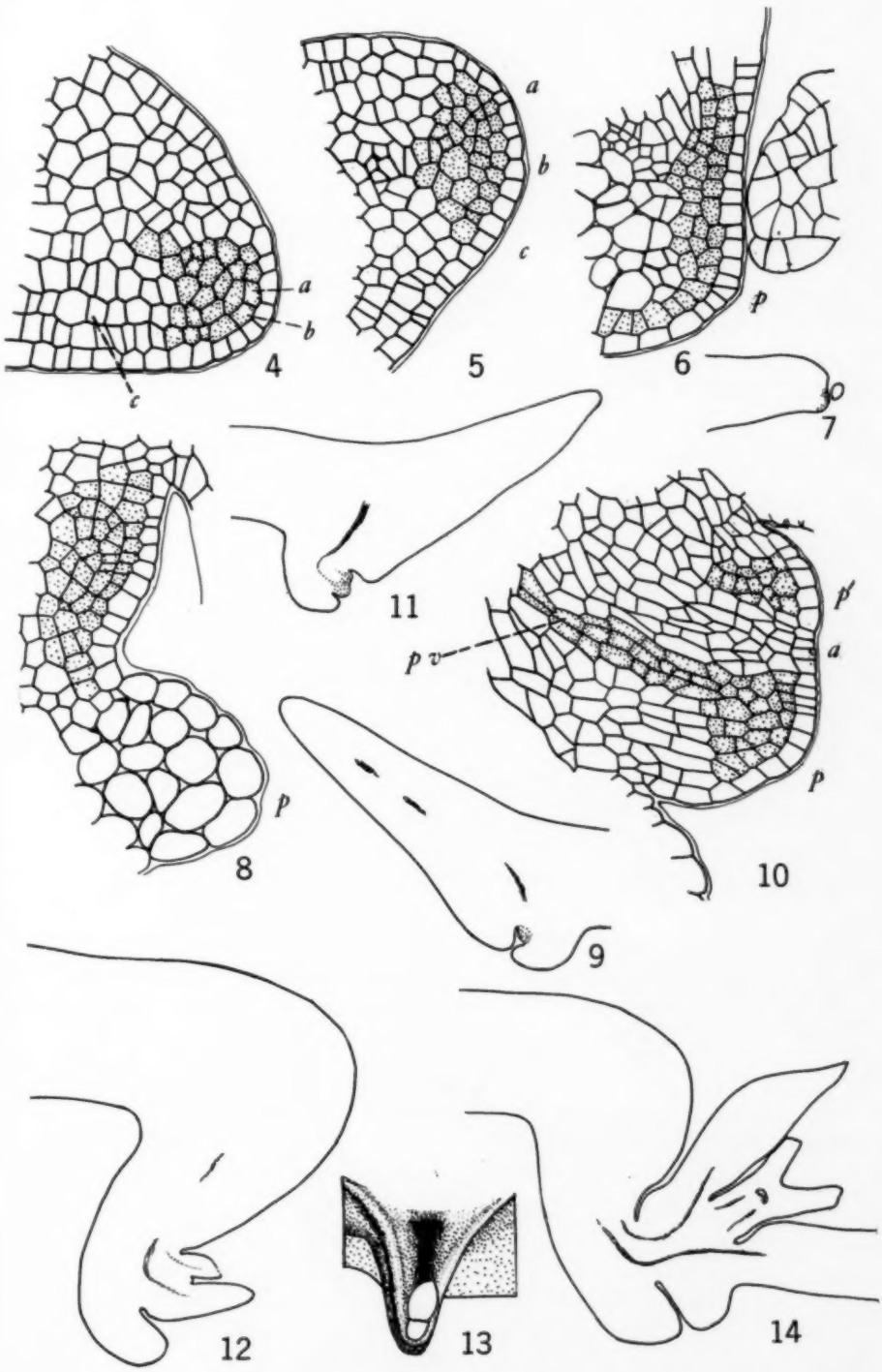
Figs. 7 and 9. Transverse sections through leaves showing portions from which figs. 6 and 8 were drawn; ×35.

Fig. 10. Section comparable to fig. 7 but further developed showing: organization of young pseudo-bulbil; *p*, primordium of first leaf; *p'*, primordium of second leaf; *a*, apical meristem of plantlet; *pv*, provascular strand; ×365.

Fig. 11. Transverse section through leaf showing position of plantlet shown in fig. 10; ×35.

Figs. 12 and 14. Transverse section through leaves showing further development of pseudo-bulbil. Fig. 12, ×35. Fig. 14, ×16.

Fig. 13. Diagram showing grooved peg with pseudo-bulbil from above; ×10.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A new Brazilian species of the genus Utricularia

EDMUND M. MERL

(WITH TWO TEXT-FIGURES)

In his paper on the variety of structure and function in the traps of *Utricularia* and *Polypompholyx*, F. E. Lloyd[1] describes among others the bladders or traps of a yet undescribed Brazilian species which, on the basis of the material supplied to me by Professor Lloyd, I regard as a new species, which I have named *Utricularia Lloydii* (Merl) in his honor.

Since we are concerned with a species interesting from various points of view, I shall present in what follows a more intimate description.

U. Lloydii occurs in the region of the Rio Branco[2] but on account of its small size is easily overlooked. The inflorescence, at most 7 cm. in height, (fig. 1) bears only one yellow flower, aside from which there is however an additional flower bud which appears usually not to develop further.

At the base of the scape there arises in its uppermore zone a number of rhizoids with short, lateral, adhesive shoots, densely clothed with sessile, knob-shaped, glandular hairs (lower pointer, fig. 1). Just below there extend stolons which carry leaves, bladders and additional secondary stolons. These secondary organs which arise from the primary stolon occur on its flanks and are lateral but nevertheless approach each other somewhat dorsally.

The apex of the stolon is straight—not, as in many other species, inrolled crosier fashion. The narrow linear leaves usually bear two to three bladders. The upper ones are usually displaced into the leaf lamina and placed at right angles to this, their openings being turned toward the apex of the leaf.

The species is particularly worthy of note, however, because of the occurrence of bladders of two sorts. (fig. 2). This peculiarity, to which Lloyd and others already have drawn attention, is shared by other representatives of the genus.[3] Nevertheless, the phenomenon is limited to only a few species. For the sake of completeness, I shall here repeat a number of details already pointed out by Lloyd. The bladders of *U. Lloydii* are extremely short-stalked, indeed almost sessile. The stolon bladders (fig. 2a) are in general of different form from those on the leaves (fig. 2b).

[1] Lloyd, F. E. 1932. The range of structural and functional variety in the traps of *Utricularia* and *Polypompholyx*. Flora **126**: 303–328.

[2] The collector's label reads: Fl. amarilla; plantinha dos terrenos arenosos e humidos. Retiro do Serra da Lira, Rio Branco. Colhido por J. Geraldo.

[3] Compare, for example, *U. volubilis* R.Br. (Merl, 1915).

The former have on their front aspect, above the entrance, two short, broad, approximately triangular antennae which bear trichomes with an elongated basal and a rather long end cell, arranged in rows. Additional rows of similarly formed trichomes extend laterally to the entrance and stand in especially dense order on a chin- or ramp-like projecting portion of the bladder beneath the entrance, occupying almost the whole lower half of the anterior part of the bladder. Similar but shorter trichomes occur

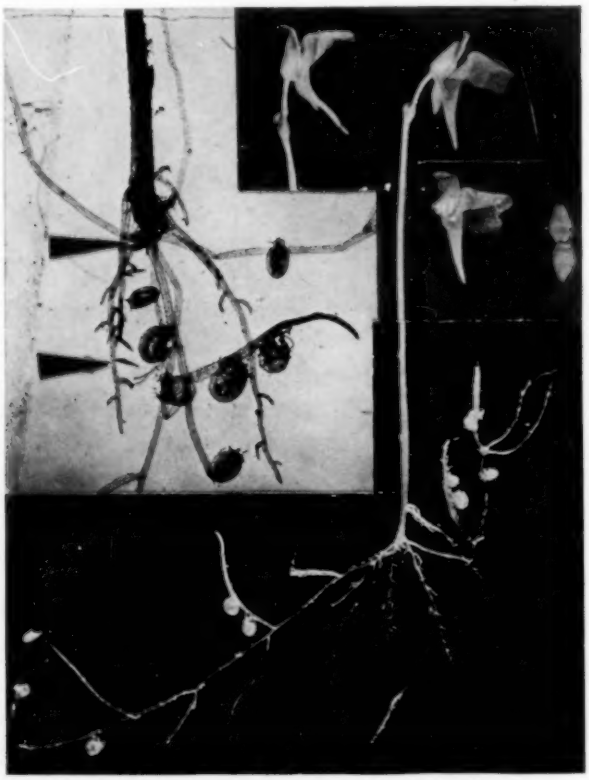

Fig. 1. *U. Lloydii* Merl. An entire plant enlarged about one-third. Above, left: the basal portion of another plant. The upper pointer indicates the seed-shell; the lower a stolon with short, fusiform branches. Above, right: other flowers and a pair of sepals.

also in the entrance on the anterior portion of the door, which is free of these in its innermore region.

Very different from the above are the bladders which occur on the leaves. These possess thinner, longer, and somewhat downwardly bent, horn-like antennae, on which there occur a number of merely sessile, spherical, glandular trichomes, such as occur on other parts of the plant,

for example on the lateral outer walls of the bladder, adhesive shoots, stolons, etc.

There is an especially strong covering of these sessile trichomes clothing the ramp. In the upper part of the entrance we find short-stalked trichomes with more elongated end cells, but in the middle of the door there is a single trichome with an enlarged basal cell and a bristle-like elongated end cell. In both kinds of bladders there occur immediately under the

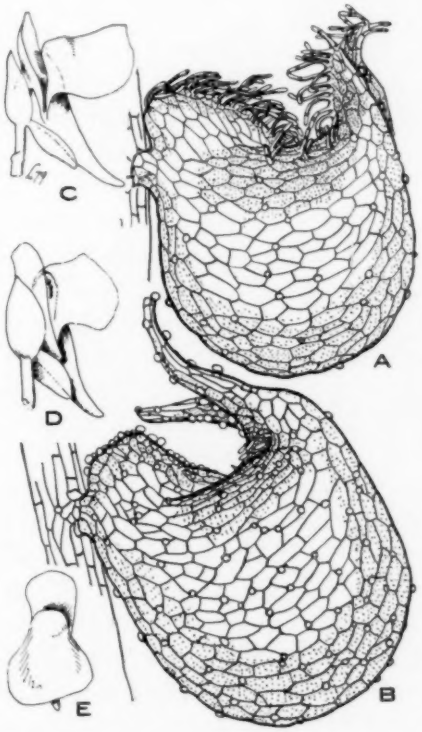

Fig. 2. *a*, bladder usually found on the stolons; *b*, bladder usually found on the leaves; *c–e*, flower in three positions.

threshold trichomes with a club-shaped end cell, following which there is a group of two-armed hairs with similar end cells, such as occur scattered on the entire inner wall surface of the bladders.

In the matter of the distribution of these two kinds of bladders there are frequent exceptions, so that where one would expect one type of bladder to occur one finds the other kind.

Since the form of the bladder is an important, if only recently apprel ciated character, useful in the identification of *Utricularia* species, it wil-

be interesting to note in what other Brazilian species we find analogous conditions to those above described.

The type of bladder with broad antennae and external files of trichomes occurs chiefly among the violet or blue flowered species of the group represented by *U. globulariaefolia* Mart. To this group I refer, in addition, the most nearly related forms, *U. Gomezii* D.C., *U. fontana* St. Hil., *U. fusiformis* Warming, lack of material of which permits scarcely more than speculation; also the species *U. tridentata* Sylven, *U. Lindmanni* Sylven, *U. ternata* Sylven, *U. bicolor* St. Hil., and *U. amethystina* St. Hil. In these species, with the possible exception of the last named, there occurs also a more or less strongly developed ramp below the entrance of the bladder. The yellow-flowered *U. modesta* D.C., displays also this type of structure. *U. Selloi* G. Weber, a species of which the bladders have not yet been described, also belongs here. This small, yellow-flowered plant recalls in many ways *U. Lloydii*. Aside from differences in the form of the flower, differences can also be recognized in that of the bladders. Whether dimorphism of the bladders occurs in *U. Selloi* G. Weber, I cannot at the moment say, since I have seen only one stolon bladder. This was relatively long-stalked with three-cornered antennae and a ramp provided with files of hairs in the usual manner. The bifid hairs of *U. Lloydii* are, however, represented by quadrifid hairs, as is usual in the other above-cited species.

The leaf bladder type occurs also in the group of species represented by *U. colorata* Benj. All its representatives, *U. colorata* Benj., *U. Meyeri* Pilger, *U. spicata* Sylven, *U. micrantha* Benj. and probably also *U. dubia* Benj. are yellow flowered and have narrow, bladder-bearing leaves with two-horned bladders without external rows of trichomes and all provided with bifid internal trichomes. The type of bladder provided with horn-like antennae is in any event of very frequent occurrence among the Brazilian *Utricullariae*, as, for example, in *U. reniformis* St. Hil. and *U. Dusenii* Sylven. *U. Lloydii*, therefore stands in the middle position between the *U. globulariaefolia-U. modesta* group on the one hand and the *U. colorata* group on the other.

The diagnosis of the species is as follows:

Utricularia Lloydii Merl sp. nov. *Utricularia* gracilis, annua, *stolonibus* capillaribus, apice rectis, ampulliferis foliiferisque. *Ampullae stolonum* (circ. 0.9×0.7 mm.) in fronte duabus antennis triangulis, glanduloso-pilosis, circa os pilis glandulosis munitae, sub ore menti instar procursu. *Folia* linearilingulata, ampullifera, circ. 5–7 mm. longa: lamina circ. 4×0.3 mm. *Ampullae superiores foliorum* in fronte cornigerae, cornibus (antennis) sub longioribus atque tenuioribus quam ampullae stolonum, sine pilis longis extraneis. *Scapus* gracilis circ. 3.8–5 cm. longus, filiformis, parte superiore 0.3–0.4 mm., parte

inferiore —0.5 mm. crassus, uni- (vel bi-?) florus, paucis (2–4). *Squamis* minutis, lanceolato-ovatis, basifixis, 0.6–0.7 mm. longis. *Bracteae* ternatae, basifixae, bractea media triangulo-ovata, 0.8–1.2 mm. longa, laterales vix conspicuae breviores, linearisubulatae. *Pedunculus* 2–3 mm. longus. *Sepala* subinaequalia, superius ovatum acutum, integrum, circ. 2.4–2.6×1.3–1.8 mm., inferius minus, ovatum, apice minute emarginatum, 2.2–2.3×1.3–1.6 mm. *Corolla* lutea; labium superius integrum, ovatum, subrotundatum, 2.4–3.4 mm. longum, 1.5–1.8 mm. latum; labium inferius integrum, subundulatum, rotundatum, porrectum, 2.8–3.0 mm. longum, diametro transverso 3.7–4.4 mm. latum; palato non valde elevato, rotundato, margine subpiloso; calcare descendente, recto, leviter sursum curvato, acuto, vel apice vix conspicuei praemorso, lab. inf. longiore, 3.6–4.5 mm. longo. Capsula ovata; semina minutissima, subglobosa, striata.

"Brasilia, ad flumen Rio Branco, Retiro do Serra da Lira, locis arenosis humidisque."

Type specimen in Herbarium of the New York Botanical Garden. Cotype: Botanical Institute, Munich.

Vegetation of the northwestern coast of Mexico

FORREST SHREVE

(WITH THREE FIGURES)

The portion of the mainland of Mexico lying along the Gulf of California and the Pacific Ocean in the states of Sonora and Sinaloa is of ecological and phytogeographic interest by reason of its displaying the transition from desert to sub-tropical thorn forest. The region is one in which the flora has not been thoroughly studied and in which the vegetation has not been described. In collaboration with the Dudley Herbarium of Stanford University, the Desert Laboratory is now conducting an investigation of the flora and vegetation of the desert region surrounding the head of the Gulf of California, comprising portions of Baja California, California, Arizona and Sonora. The present paper embodies a very brief discussion of a part of this territory and of the region immediately south of it with respect to the relations between desert and thorn forest.

Arid conditions prevail from eastern Washington southward through the Great Basin and Mohave Desert to the mouth of the Colorado River, thence continuing along both sides of the Gulf of California into the tropical zone. The pronouncedly desert conditions found north of Lat. 28° are gradually ameliorated by a heavier and better distributed rainfall in the Southern District of Baja California and on the Mexican mainland south of Sonora. A comparison of the northern and southern extremities of the desert reveals an almost complete difference in flora and dissimilarity in the character of the vegetation. In addition to the gradual changes that are found in going south in the Great Basin there is a marked transition in the vegetation in southern Nevada, where a rapid fall in elevation accompanies the supplanting of *Artemisia tridentata* by *Larrea tridentata* and *Franseria dumosa* as the most abundant plants. The transition from desert to thorn forest in southern Sonora brings within a distance of 200 km. a change in the plant life almost as great as that found in the 2400 km. from the Columbia River basin to the valley of the Rio Sonora.

Extensive intermont plains occupy southwestern Arizona and the western half of Sonora, gradually narrowing to a belt only 40 to 60 km. in width throughout the length of Sinaloa. It is in the coastal fringe of the desert below 500 m. elevation that the most comparable locations are found for observing the changes in vegetation which mark the southern limit of the North American desert on the Pacific slope.

The region adjacent to the lower course of the Colorado River has a rainfall of less than 125 mm. (5 in.) per year, and certain parts of it have the thinnest plant covering to be found in North America. The principal

plants of this region are *Larrea tridentata* and *Franseria dumosa*. In many large valleys they outnumber all other perennial plants 50 to 1. In spite of the marked difference in the vegetative characters of these plants they are closely parallel in the variation of their size and abundance from place to place. They are often the dominants in all situations and all types of soil. It has been estimated in several localities that if the crowns of these shrubs and all of their associates were projected on the ground their collective area would be from 4 to 15% of the total surface. Other perennials occur-

Fig. 1. Typical landscape in the deserts bordering the lower course of the Colorado River, with *Larrea tridentata* and *Franseria dumosa*.

ring in such situations are *Bebbia juncea*, *Petalonyx thurberi*, *Opuntia ramosissima*, *Encelia frutescens* and *Atriplex canescens*. On sandy soil the grass *Hilaria rigida* is abundant, forming large tufts. Where small streamways cross the plains there is a great increase in the number of plants per unit area as well as in the number of species present. Here only are small trees found including *Cercidium torreyanum*, *Olneya tesota*, *Prosopis velutina* and *Parosela spinosa*, as well as the shrubs *Acacia greggii*, *Lycium andersonii* and *Hymenoclea monogyra*.

South of the Gila River the plains of Yuma Co., Arizona, exhibit a somewhat higher type of desert vegetation. The percentage of ground cov-

ered is higher, although the vegetation is still very open, the average height of the perennials is greater, the number of frequent species rises to 15 or 20, the differentiation of the vegetation of the various habitats is higher, and there are representatives of several vegetative types. In these areas *Larrea* and *Franseria* are still present but together form only about 60% of the plant population. Their commonest associates are *Olneya tesota*, *Encelia farinosa*, *Acacia greggii*, *Cercidium torreyanum*, *Hilaria rigida*, *Opuntia ramosissima*, *O. bigelovii*, *Echinocereus engelmannii* and *Krameria grayi*. A complete list of the large perennials of these plains would include about 30 species.

The two similar types of vegetation which have been described are found, with minor variations, throughout the plains of southwestern Arizona and northwestern Sonora as far south as Lat. 30°. In the lower drainage of the Magdalena (Concepcion) River, *Larrea* occurs in extensive stands with no *Franseria dumosa* and few other plants, or in other localities with *Franseria deltoidea*. A few new perennials are added to the flora between the Gila and Magdalena Rivers but none of them are important components of the vegetation of the plains. Among these are *Elaphrium microphyllum*, *Jatropha spathulata*, *Sapium biloculare*, *Cordia greggii*, *Lophocereus schottii*, *Colubrina glabra* and *Lycium richii*.

In the region between the Magdalena and Sonora Rivers the vegetation remains very open but increases slightly in its average height and considerably in the number of abundant species. *Larrea* becomes more closely confined to the immediate coast and to certain restricted habitats, while *Franseria dumosa* reaches its southern limit. The species which are here dominant throughout the plains are chiefly ones that occur north of the Gila River but are there confined to streamways, hills or coarse outwash slopes. The principal change from Lat. 34° to Lat. 30° is therefore the elimination of the highly xeromorphic dominants of the former region and the emergence of the slightly less xeric species from their restricted habitats into the position of dominance. This involves *Olneya tesota*, *Cercidium torreyanum*, *Prosopis velutina*, *Celtis pallida*, *Condalia spathulata*, *Encelia farinosa*, *Lycium andersonii*, *Lemaireocereus thurberi*, *Cercidium microphyllum*, *Acacia greggii*, *Jatropha cardiophylla* and *Elaphrium microphyllum*. Species first appearing in this section of the coast and of importance in the aspect of the vegetation are *Cercidium sonorae*, *Acacia occidentalis*, *Fouquieria macdougalii*, *Pachycereus pringlei*, *Opuntia thurberi*, *Jatropha cinerea* and *Guaiacum coulteri*. The general aspect of the vegetation is determined by the legminous trees *Olneya*, *Prosopis* and *Cercidium*, and by the shrub *Encelia*. As *Larrea* disappears its place as the most abundant and ubiquitous plant is taken by *Encelia*. Cacti are frequent enough to

lend character to the landscape but form a very small percentage of the plant population. *Opuntia fulgida* is locally abundant but often absent over areas of hundreds of hectares. *Opuntia thurberi* occurs frequently but is nowhere abundant. *Lophocereus schottii* and *Lemaireocereus thurberi* are of frequent occurrence but not continuously within range of the eye. *Rathbunia alamosensis* is abundant only in thickets along the streamways.

From the Sonora River southward nearly to the Yaqui River there is little change in the physiognomy and composition of the vegetation just described. There are still all of the characteristics of the less pronounced

Fig. 2. Open type of arboreal desert near Moreno in central Sonora, with *Prosopis velutina, Ichthyomethia mollis* and *Encelia farinosa.*

type of desert. The plants are widely spaced, the height of the tallest trees is from 4 to 5 m., trees and shrubs are of strongly xeromorphic character, succulents are frequent, the vegetation is denser along the streamways than elsewhere, annuals and seedling perennials are abundant chiefly in the shade of the largest trees. This belt is noteworthy for the first appearance of *Acacia macracantha*, which is the dominant tree of the thorn forest for hundreds of kilometers to the south, and for the last occurrence of *Larrea*, as a plant of minor importance in the vegetation of alluvial flats near the coast 8 km. east of Empalme. The larger streamways of this belt are fringed with trees from 3 to 5 m. higher than the general level, or are bordered by thickets. Like the analogous situations far to the north these slightly more favorable habitats induce heavier stands of the plants

common to the region and also support the northernmost examples of many perennials. At about Lat. 28°30′ these situations begin to bear dense thickets of vegetation, with trees, shrubs, herbaceous perennials, cacti and vines, all forming communities such as do not exist further north, and giving a strong forecast of the vegetation found further south. Some of the trees of the riparian thickets are *Acacia macracantha*, *Guazuma ulmifolia*, *Ichthyomethia mollis*, *Pithecolobium sonorae*, *Vitex mollis*, *Coursetia glandulosa* and *Haematoxylon brasiletto*. The arborescent *Pachycereus pecten-aboriginum* here finds its northern limit while *Rathbunia* and *Opuntia thurberi* grow in great profusion, partly supported by the shrubbery. Other woody plants common in the thickets of this belt are *Lantana camara*, *Euphorbia plicata*, *Karwinskia humboldtiana*, *Cordia greggii*, *Mimosa grahami*, *Cassia biflora*, *Paullinia sonorensis* and *Vallesia glabra*.

Between Lat. 28°, in the vicinity of Guaymas, and Lat. 27°, in the vicinity of Navojoa, comes the rapid change which marks the southern limit of the desert. The riparian thickets become more extensive, and the open patches suggestive of desert spacing become fewer. In certain situations, however, they may still be seen as far south as the valley of Rio Fuerte, in Sinaloa, with *Cercidium*, *Encelia* and *Opuntia fulgida* as their characteristic plants. The increase in density involves both trees and shrubs. The maximum height of the vegetation increases slightly. Where there is relative simplicity in the composition, due to the prevalence of *Acacia macracantha*, there is a uniform canopy. More often, however, the sky line is very irregular, due to the increasing complexity of composition and to the difference in the height attained by the secondary trees. The vegetation is nowhere dense enough to bring about the elimination of all but the tallest trees.

The thorn forest is at best a xeric type of vegetation. Its trees rarely exceed 10 m. in height, while the average for the dominants is 7 to 8 m. The crown is rarely dense enough to eliminate small shrubs and root perennials. The trees branch widely and have sparse foliage. The leaves of the common trees are small or more often compound with small leaflets. Cacti are more abundant in the thorn forest than they are in most of the coastal territory between the Magdalena and Yaqui Rivers. Spines and thorns are very prevalent. In spite of these xeric features the thorn forest is rather sharply differentiated from the desert, as it has been characterised in a previous paragraph. Not only does the vegetation serve as a criterion of the difference but also the nature of the weathering, the condition of the soil surface, the accumulation of litter, the evidences of run-off, the character of both the smaller and larger drainageways, and the physiographic influences of wind.

In the thorn forest of the southernmost part of Sonora *Acacia macracantha* is the commonest tree, forming approximately 60 per cent of the stand. It has several important associates which are sporadic in occurrence and uneven in abundance, although there are no easily recognised variations of soil or other features to which their presence can be attributed. Prominent among the secondary trees and other large plants are *Ichthyomethia mollis*, *Cercidium sonorae*, *Ipomoea arborea*, *Zizyphus sonorensis*, *Pachycereus pecten-aboriginum*, *Prosopis glutinosa*, *Ceiba acuminata*, *Cassia biflora* and *Coutarea pterosperma*.

Fig. 3. Typical thorn-forest 46 miles east of Cajeme in southern Sonora, with *Acacia macracantha*, *Pachycereus pecten-aboriginum* and *Franseria cordifolia*.

For 500 km. south of Navojoa, to the southern boundary of Sinaloa, the coastal region is narrow, consisting mainly of mature outwash slopes from the adjacent mountains, crossed frequently by alluvial belts bordering the large rivers. Throughout this distance the physiognomy of the vegetation is almost identical. There is a slight increase in the density, particularly that of the shrubs and other undergrowth, south of the Rio Elota, but the height, character of canopy, nature of the foliage and other general features undergo little change. Many of the common plants of central Sonora do not extend to the southern end of Sinaloa, as *Cercidium torreyanum*, *C. sonorae*, *Olneya tesota*, *Fouquieria macdougalii*, *Encelia farinosa*, *Lemaireocereus thurberi*, *Forchammeria watsoni*, *Lophocereus schottii* and *Pithecolobium sonorae*. A dominant place is held by *Acacia macra-*

cantha, *Ipomoea arborea* and *Zizyphus sonorensis* throughout Sinaloa, and several new secondary trees appear, notably *Lonchocarpus megalanthus*, *Bauhinia longiflora*, *Crescentia alata*, *Bunchosia palmeri* and *Caesalpinia cacalaco*. The commonest of the shrubs is *Croton alamosanus*. Striking features of the vegetation in southern Sinaloa are the frequence of native palms, several epiphytic species of *Tillandsia*, and also numerous terrestrial bromeliads. The alluvial plains bear scattered examples of trees of much greater height and size than those of the thorn forest.

In considering the physical conditions which control the vegetation through the 1500 km. from the Bill Williams valley in western Arizona to the valley of the Rio Union in southern Sinaloa it is obvious that both rainfall and temperature are of great importance. There is a gradual increase in the annual precipitation from a range of 50 to 125 mm. (2 to 5 in.) north of the Magdalena River, and 250 to 375 mm. (10 to 15 in.) between there and the Yaqui River, with a marked increase in southern Sinaloa to 722 mm. (28.42 in.) at Mazatlan. The percentage of the annual total which falls in the summer months increases from 25 in the north and 75 in southern Sonora to 77 in southern Sinaloa. Much of the importance of the increasing rainfall for plants is offset by the rising temperature and increasing length of the hot period which accompanies it. The transition from desert to thorn forest coincides very nearly with the attainment of an annual rainfall of 375 mm. (15 in.). This is a datum, however, which is of little importance except in connection with accompanying conditions.

With reference to temperature it must be noted that the entire area under discussion is subject to high daytime ranges during six to nine months of the year, according to latitude. Frost is of annual occurrence north of the Magdalena, but becomes less frequent through southern Sonora. It is infrequent at Cajeme (Ciudad Obregon), Son., and rare at Los Mochis, Sin., being unknown further south.

The short distance within which desert gives way to thorn forest, as contrasted with the extended range of each of these vegetations to the north and south, seems to indicate the operation of a potent group of controlling conditions. The rise of rainfall, particularly in the summer months, the change from a continental to a coastal position (due to the location of the southern end of the peninsula of Baja California), the decreasing distance from tide water to a high mountain background, and the absence of frost are undoubtedly all concerned. The plants of southwestern Arizona are both drought resistant and cold resistant. Those of Sinaloa are drought resistant only. It appears highly probable that the winter temperature conditions have strongly limited the number of drought re-

sistant plants that have been able to enter the desert, and that the relatively small flora of the desert is not to be attributed solely to adverse moisture conditions.

SUMMARY

The most arid region in North America lies along the lower course of the Colorado River and on both sides of the head of the Gulf of California. In portions of this region *Larrea tridentata* and *Franseria dumosa* form 98% of the vegetation but often cover only 4 to 15% of the ground surface. The less frequent plants are confined to streamways, coarse outwash and mountain slopes, but almost all of them are found in the vegetation of the plains in Sonora south of Lat. 30°. There the dominant plants are *Olneya tesota*, *Cercidium torreyanum*, *Prosopis velutina* and *Encelia farinosa*.

On going south from central Sonora there is a steady increase in the number of common perennials and in the number of vegetative types that are represented. Cacti are locally abundant but often absent over large areas or found only as occasional large individuals.

At about Lat. 28°30′ the vegetation of streamways and alluvial plains begins to be much more dense and many new trees and shrubs are found in such situations, the majority of them being forms that are dominant in the general vegetation further south. Between Lat. 28° and Lat. 27° there is a rapid change in the character of the vegetation, which here becomes denser, taller and richer in composition, at the same time that a few less xeromorphic species appear. This is the region of transition from desert to the arid type of thorn-forest which extends southward from the Mayo River to southern Sinaloa, with little change in its physiognomy and ecological characteristics but with constant additions to its flora.

It is within a relatively short distance that the extended area of desert merges into thorn-forest, a type of vegetation also of wide distribution on the Pacific coast of Mexico. The transition coincides closely with the attainment of an annual rainfall of 375 mm. and the disappearance of frost.

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Haploid chromosomes of Riccia glauca

D. A. JOHANSEN

(WITH TEXT-FIGURE)

Riccia glauca L. is increasingly coming into favor among instructors as being more satisfactory than *Ricciocarpus natans* for the demonstration of the origin and development of the sex organs and spores in a simple liverwort. Some instructors, requiring the observation of greater detail than do others, have met with difficulty when attempting to demonstrate the reduction of the chromosome number during spore formation. The trouble is that the haploid number of chromosomes, as judged from the scanty literature available, appears to be in dispute. The present paper constitutes an attempt to provide an answer to the question as to exactly how many haploid chromosomes *Riccia glauca* possesses.

Beer (1906) states that "The reduced number of chromosomes . . . is either seven or eight, but it could not be decided with certainty between these two numbers." Heitz (1927), using his peculiar boiling method, claims to have found nine haploid chromosomes, while Miss Wentzel (1929) cites the number as being eight.

During the past few years the writer has prepared many hundreds of slides of *R. glauca* for class purposes. While checking over and classifying these preparations, all slides showing the reduction divisions in the spore mother cells were set aside for future study. In this manner a collection of about 60 slides, representing approximately the same number of individual plants, has accumulated and forms the basis of the following report.

The plants were collected at various localities in west-central California, and at one locality in Southern California. Except for the larger size of the southern plants, they were much alike and showed no apparent cytological differences.

Fixation in some cases was with a formalin—acetic acid—50% alcohol mixture; in others, the plants were allowed to remain in Carnoy's fluid for not more than six minutes and were then transferred to Navashin's fluid. The sections were cut at 12 microns. Some slides were stained with iron haematoxylin, others with methyl violet and erythrosin by the picro-alcohol method.

In all cells showing the early first metaphase in polar view (fig. 1), eight chromosomes are to be found. The chromosomes may be divided into three size groups, namely, two large chromosomes, five of a slightly smaller size and a single tiny globular element. The tiny chromosome divides precociously at mid-metaphase (fig. 2). During the anaphase (fig. 3), the two

tiny chromosomes, which go to opposite poles, invariably precede all the other chromosomes. The two larger chromosomes lag behind the five in the next size group, and one of the two has frequently been observed to delay final separation until all the other chromosomes have already reached their respective poles and the interphase is about to occur.

The writer feels convinced that the true haploid number of chromosomes in *Riccia glauca* is eight. Beer (1906) plainly had difficulty in recognizing the tiny eighth chromosome. As for the count of nine claimed by Heitz (1927), there are two possible explanations. The less probable one

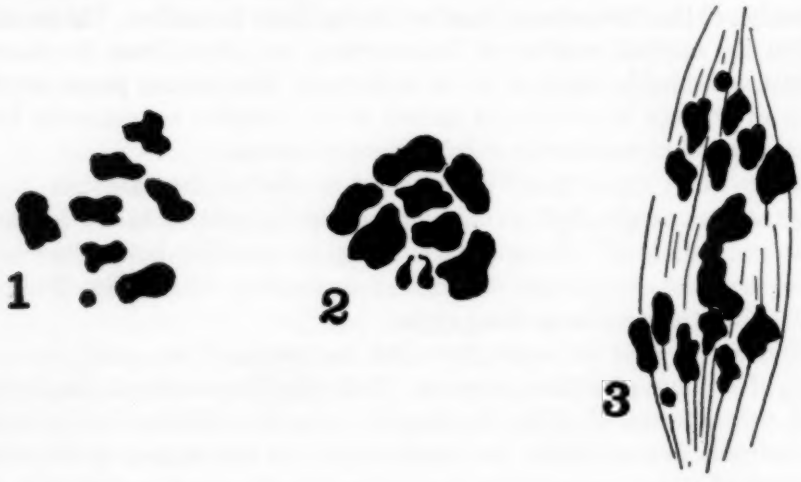

Fig. 1. Early metaphase I in spore mother cell of *Riccia glauca*. Fig. 2. Late metaphase I showing division of tiny eighth chromosome. Fig. 3. Anaphase I showing delayed separation in one of the two large bivalents. ×4400.

is that his observations were made at late metaphase after the tiny globular element had divided. It appears more likely however, to judge by the badly shrunken appearance of the chromosomes in his fig. 61, that fixation was so incredibly poor that a misinterpretation was made. Only one large chromosome is shown, whereas in the writer's preparations two large elements were always observed. It is probable that the two vertically oriented chromosomes at the left in the figure cited are in reality a single chromosome, as their combined length about equals that of the one large chromosome. Miss Wentzel (1929) claims that her "Figur 8 zeigte die Polansicht einer Anaphase mit 8 Chromosomen." The figures are so badly reproduced as to be useless; in this particular figure, the stage appears to be the metaphase but the chromosomes are indistinguishable from the dots used for

stippling. The same criticism applies to her figures 7 and 9, in which "In die seitlichen Ansichten der Spindeln sind bei einer Einstellung des Mikroskops 3–5 Chromosomenpaare zu sehen."

The writer is indebted to Mr. Louis C. Wheeler for the material from Southern California, and to Dr. Peter Claussen of Marburg, Germany, for invaluable assistance with certain literature which would otherwise have been unavailable.

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A revision of the subgenus Hugelia of the genus Gilia (Polemoniaceae)

THOMAS CRAIG

(WITH PLATE 23)

This study, carried on at the Pomona College Herbarium, was undertaken at the suggestion of Dr. P. A. Munz. I am very much indebted to him for guidance and assistance throughout this undertaking, and I am also indebted to the following persons for supplying notes and for lending herbarium specimens: Dr. H. L. Mason and Elizabeth Crow Norland of the University of California (C.), Miss Alice Eastwood of the California Academy of Sciences (C.A.), Dr. Aven Nelson of the University of Wyoming (Wyo.), Dr. Wm. R. Maxon of the United States National Herbarium (U.S.), Mr. Frank Peirson of Pasadena (F.P.), and Dr. C. B. Wolf of Rancho Santa Ana (S.A.). The abbreviations in parentheses are those used in the citation of specimens. I have also visited the herbaria of Stanford University (S.), and the Santa Barbara Museum (S.B.), in order to study the collections of Hugelia in these herbaria. In addition to the work carried on in the herbarium, much time and effort have been spent in the field; I have seen a large percentage of the forms growing.

HISTORY OF THE SUBGENUS

The history of the subgenus Hugelia has been reviewed by Macbride, Cont. Gray Herb. n.s. **49**: 54. 1917. Therefore, for the sake of brevity, I am giving only the following short synopsis to cover the history of the group.

HUGELIA

Hugelia, as a new genus, was proposed by Bentham, Bot. Reg. **19**: sub. t. 1622. 1833, in honor of Baron Charles de Hügel of Vienna. As section, Gray Proc. Am. Acad. **8**: 272. 1870. As subgenus under *Gilia*, Milliken, Univ. Calif. Pub. Bot. **2**: 24, 38–40. 1904. As subgenus under *Navarretia*, Brand, Pflanzenreich IV, **250**: 164–168. 1907. *Eriastrum*, Wooton & Standley, Contrib. U. S. Nat. Herb. **16**: 160. 1913. *Welwitschia*, Rydb., Fl. Rocky Mts. 688, 1065. 1917. *Hugelia* as section under *Gilia*, Macbride, Cont. Gray Herb. n.s. **49**: 54. 1917. As genus, Jepson Man. Fl. Pls. Calif. 792–793. 1925.

I cannot agree with Brand in his inclusion of *Hugelia* in *Navarretia*, while at the same time separating both from *Gilia*, even though the diffusely branched *G. filifolia* var. *typica* and *Navarretia Abramsii* are so closely related as to appear almost conspecific; for other *Hugelias* are also

closely related to other groups of *Gilias*. *Gilia filifolia* var. *diffusa*, especially in plants from Utah and Texas, very closely approximates *G. Gunnisonii*. *Gilia densifolia* is rather close to *G. Wrightii*, and *G. eremica* is much like a *Langloisia*. Because these groups are all so closely related, and because of the lack of absolute characters to separate the groups, I believe it better to regard *Hugelia* not as a part of the genus *Navarretia*, as done by Brand; nor as a separate genus, as done by Jepson, l.c., but as a subgenus of *Gilia*.

KEY TO SPECIES

A. Woody-based perennial; corolla 15–30 mm. long; the tube 2–3 times longer than calyx.

1. *G. densifolia.*

AA. Annual; corolla 7–18 mm. long; the tube rarely longer than calyx, never more than twice as long.

B. Flowers yellowish; the corolla lobes almost equalling the tube; anthers more than 1½ mm. long. Central & So. Calif. cismontane region and high desert slopes of So. Mts.

3. *G. lutescens.*

BB. Flowers not yellow, or if yellowish, as is rarely the case with forms from desert regions, the corolla lobes are half the length of the tube, and the anthers 1 mm. or less long.

C. Free portions of shortest stamen at least as long as corolla tube; corolla lobes as long as tube, blue or pale lavender. Cismontane and high desert regions of So. California.

2. *G. virgata.*

CC. Free portions of the shortest stamen not more than two thirds the length of the corolla tube.

D. Corolla 6–8½ mm. long, commonly 7 mm. Anthers ½–1 mm. long.

E. Stems erect from base.

F. Lower cauline leaves 3–5-lobed, the lobes commonly at least ½ mm. broad.

8. *G. Wilcoxii.*

FF. Lower cauline leaves entire or 3-lobed, the lobes less than ¼ mm. broad.

7. *G. filifolia.*

EE. Stems decumbent from base.

7. *G. filifolia.*

DD. Corolla 10 mm. long or longer, commonly 12–17 mm. Anthers rarely less than 1 mm. long, commonly about 2 mm.

E. Flowers quite irregular, the free portion of shortest stamen less than half as long as the free portion of longest stamen.

6. *G. eremica.*

EE. Flowers regular or nearly so, stamens of almost equal length.

F. Lower cauline leaves 3–7-parted, most commonly 5-parted.

G. Flowers deep blue violet, lobes rarely less than two thirds as long as tube; leaf lobes commonly slender filiform, commonly up to 10 mm. long. Central Calif. valleys.

4. *G. pluriflora.*

GG. Flowers pale vivid blue or lavender, the lobes not more than ½ length of tube. Leaf lobes rarely slender filiform and rarely more than 8 mm. long.

H. Corolla 10–13 mm. long, commonly 11 mm. Anthers 1 mm. or less in length. N. E. Calif., Nev., Utah, and Northward to Wash. and Idaho.

8. *G. Wilcoxii.*

HH. Corolla 14½–17 mm. long. Anthers 1 mm. or more in length. Southwestern Mojave Desert.

5. *G. Sherman-Hoytae.*

FF. Lower cauline leaves commonly entire or with two basal lobes, very rarely with an occasional leaf with 4 basal lobes.

G. Stamens of slightly unequal length, corolla pale blue or lavender. Arizona.

6. *G. eremica.*

GG. Stamens sub-equal, corolla deep blue. Calif.

2. *G. virgata.*

TREATMENT OF SPECIES

1. GILIA DENSIFOLIA Benth., in D. C., Prodr. **9**: 311. 1845. *Hugelia densifolia* Benth., Bot. Reg. 19: sub. t. 1622. 1833; *Navarretia densifolia* (Benth.) Brand, Pflanzenreich IV, **250**: 165. 1907; *Gilia Hugelia* Steud., Nom. ed. 2, **1**: 683. 1840.

Erect perennial herb, 8–90 cm. high, much branched from woody base, glabrous to canescent lanate; stems rigid; leaves 1–6 cm. long, lanceolate to almost ovate in outline, pinnatifid into subulate spinulose or pungent lobes, rarely narrowly linear and entire; inflorescence capitate-glomerate, pilose to densely lanate; calyx from ⅓ the length of the tube to almost equalling it; corolla salverform, 15–30 mm. long, the oblong lobes ½–⅓ the length of the tube, deep violet blue to pale lavender; stamens inserted just below the sinuses, not exceeding lobes; anthers sagittate, 1.5–2.5 mm. long; filaments 4–5 mm. long; capsule 3–4 mm. long.

The perennial habit of this species distinguishes it from all other species of *Hugelia*. The only possible sources of confusion are occasional specimens of *G. virgata* var. *dasyantha* Brand., which plants, due to fall and winter rains, will on rare occasions survive and bloom in late winter and thus remotely resemble a perennial. The species is common in Central, Southern, and Lower California.

KEY TO VARIETIES

A. Corolla 22–32 mm. long. Plants from sea level—1500 ft.

B. Corolla 25–32 mm. long, lobes one third as long as tube, plants lanate; from Santa Ana River Wash. in So. Calif. at elevations of 500–1500 ft.

1b. *G. densifolia* var. *sanctorum*.

BB. Corolla 22–25 mm. long, lobes almost ½ as long as tube, plants glabrous or nearly so. Coastal San Luis Obispo & Santa Barbara Counties.

1c. *G. densifolia* var. *typica*.

AA. Corolla 14–19 mm. long. Plants from sea level—8000 ft.

B. Leaves commonly recurved, pinnatifid; the lobes about as long as width of rachis; fls. pale blue or lavender. Plant canescent lanate. Mohave Desert.

1e. *G. densifolia* var. *mohavensis*.

BB. Leaves usually ascending, lobed or entire; the lobes 2–10 times as long as width of rachis; fls. deep blue. Plant lanate to sub-glabrous.

C. Bracts of fl. clusters sometimes entire, commonly 3–5-lobed, very rarely 7-lobed; plants 20–90 cm. high; many axillary clusters, which are rarely more than 10-flowered, never more

than 15-flowered, leaves lobed or entire. Plant always remaining thinly canescent-lanate in age. Coastal and interior valleys below 4000 ft.

1a. *G. densifolia* var. *elongata*.

CC. Bracts of fl. clusters commonly 5–9-lobed; plants 15–45 cm. high; flower clusters mainly terminal, commonly 15-flowered sometimes as much as 20-flowered; leaves 2–15-lobed, never entire. Plant not uncommonly sub-glabrous. So. Calif. Mts. from 4000–8000 ft.

1d. *G. densifolia* var. *austromontana*.

1a. GILIA DENSIFOLIA Benth., var. ELONGATA (Benth.) Gray ex Brand, Pflanzenreich IV, **250**: 165. 1907; *Hugelia elongata* Benth., Bot. Reg., l.c. *Gilia elongata* (Benth.), Steud, Nom. ed. **2, 1**: 683. 1840; *Navarretia densifolia* subsp. *elongata* Brand, Pflanzenreich IV, **250**: 165. 1907; *Gilia densifolia* var. *elongata* (Benth.) Gray ex Brand, l.c.

Plants 20–90 cm. high, canescent-lanate when young, remaining so at least in the upper half until maturity; leaves ascending, rarely narrowly linear or, more commonly, with linear spinulose lobes more than twice the width of the rachis; flower clusters comparatively small rarely as much as 15-flowered, lateral as well as terminal; corolla deep blue to deep blue-violet, 15–16 cm. long, very rarely 20 mm. long; lobes half the length of the tube; stamens 4½–5 mm. long.

Type locality, California, the type collection having been by Douglas, hence from coastal region between Santa Barbara and Monterey. Ranging at lower elevations along the coast from San Luis Obispo Co. to Lower Calif. and into the interior as far as San Bernardino Valley and Southern Mohave Desert. Representative material studied: CALIFORNIA: Monterey Co., Tassajara, *Dudley* in 1901 (S); Paloma Creek, Santa Lucia Mts., *Bacigalupi* (S). San Luis Obispo Co., Templeton, *Abrams* 5044 (P); Creston, *Feudge* 1743 (P). San Benito Co., Hernandes, *Lathrop* in 1902, and 1903 (S); Cooks 7 mi. from Pinnacles, *Abrams* 6702 (S). Kern Co., Between Bakersfield and Bodfish, *Abrams* 5349 (S). Santa Barbara Co., Near Lompoc, *Mc Minn* 1047 (S); Santa Inez River, San Marcos Ranch, *Hoffmann* (S.B.). Los Angeles Co., Roscoe, *McFadden* in 1931 (C); Saugus, *Munz* and *Johnston* 11,132 (P); Pacoima Wash, San Fernando, *Munz* 9387 (P); Junction Soledad & Mint Canyon Roads, *Craig* 462 (P); Mint Canyon, *Craig* and *Hilend* 525 (P); Aliso Canyon, *Barber* 202 (C), Soledad Canyon 8 mi. W. of Ravenna, *Craig* 2007 (P). San Bernardino Co., West Slope Cajon Pass, ¼ mi. from Summit, *Craig* 1470 (P); 1 mi. from Summit, *Craig* 1471 (P); Cajon Pass, 1 mi. above Camp Cajon, *Craig* 1472 (P);

Cajon Pass ½ mi. below Camp Cajon, *Craig* 1473 (P); Cajon Pass 1 mi. above Devore, *Craig* 1474 (P); Cajon Pass Wash at Highland Blvd., *Craig* 1475 (P).

The last two numbers cited are intermediate with *sanctorum* as are all the following numbers from this County. Colton, *Wilder* in 1904 (P), *Hall* 157 (C); Banning, *Jones* in 1903 (P); San Bernardino, *Abrams* 1963 (P), *Parish* in 1888 (C); Etiwanda, *Jones* in 1925 (P). LOWER CALIFORNIA: Tecate, *Orcutt* in 1885 (C), *Orcutt* in 1883 (C). (Shows a tendency toward *austromontana*.)

The following specimens are intermediate between *elongata* and *austromontana:* Los Angeles Co., Acton, Mt. Gleason, *Elmer* 3692 (P); Ravenna, *Brandegee*, June to Aug. LOWER CALIFORNIA: Mts. of Northern Lower Calif., *Orcutt* (C);San Pedro Martir Mts., *Robertson* 49(C). CALIFORNIA: San Diego Co., Jacumba, *Cleveland* in 1884; Eastern base San Jacinto Mt., *Hall* 1861 (C); Old Nicolas Canyon, *Munz* 5924 (P, C). Riverside Co., between Vandeventer and Hemet Valley, *Munz* 5820 (C, P); El Toro Mt., *Van Deventer*, in 1901 (C). NEVADA: Nye Co., Pahute Peak, *Purpus* in 1897.

1b. GILIA DENSIFOLIA VAR. SANCTORUM Milliken, Univ. Calif. Pub. Bot. **2**: 39. 1904. *Hugelia densifolia* var. *sanctora* (Mill.) Jeps., Man. Fl. Pls. Calif., 792. 1925.

Plant 25–75 cm. high, woody at base, entire plant, except old woody portions, lanate even in age, densely so when young; flowers blue, 25–32 mm. long; corolla-lobes one third as long as the tube.

Type locality, Spanish town crossing above Riverside. The variety in its best development is found in the river bottoms of the Santa Ana River and its tributaries from near Highland, San Bernardino Co. (El. about 1500 ft.), to Rancho Santa Ana, in Orange County (El. 500 ft.). Representative material studied, CALIFORNIA: San Bernardino Co., Santa Ana River near East Highland, *Feudge* 1569 (P); Plains near San Bernardino, *Lemmon* in 1876 (C); San Bernardino, *Parish* 4178 (C); Lytle Creek near San Bernardino, *Parish* 7139 (P, C). Riverside Co., Santa Ana River bottoms, *Reed* in 1910 (P); Santa Ana River near Spanish town crossing, *Hall*, 173 & 683, type (C). Orange Co., Rancho Santa Ana, *J. T. Howell* 2985 (P, S.A.).

1c. **Gilia densifolia** var. **typica** n. nom. *Hugelia densifolia* Benth., Bot. Reg. 19: subt. 1622. 1833. *Gilia densifolia* Benth., in D. C., Prodr. 9: 311. 1845.

Plant 20–30 cm. high, glabrous to sub-glabrous; leaves entire or divided; flower clusters large, mainly terminal, often 25-or-more-flowered; corolla 22–25 mm. long; the lobes about 8 mm. long.

Type locality, California, the type collection having been made by Douglas, hence from the coastal region between Santa Barbara and Monterey. A photograph of this type and one of *elongata* have been obtained from Kew. Representative material studied, CALIFORNIA: San Luis Obispo Co., Haynes Ranch, *Ingalls* in 1912 (C.A.); Sand Hills 2 mi. south of Pismo Beach, *Peirson* 2224 (F. P. P.); Morro Sands, *Eastwood* 14,944 (C.A.). Santa Barbara Co., Beach near Santa Maria, *Eastwood* 867 (C.A.); 3 mi. north of Guadelupe, *Craig* 1926 (P).

The following collections are intermediate between var. *elongata* and var. *typica:* Santa Barbara Co., Lompoc, *Hoffmann* (S.B.); Mesa 3 mi. east of Lompoc, *Breneiser* in 1933 (P); 14 mi. E. of Santa Maria, *Craig* 1873 (P).

This variety resembles var. *sanctorum* in the largeness of its showy flowers. It is however amply distinct in being glabrous or sub-glabrous and in having the corolla lobes longer in relation to the tube, as well as in its more northern range.

1d. **Gilia densifolia** Benth. var. **austromontana** Craig n. var. *Navarretia densifolia* subsp. *eu-densifolia* Brand., Pflanzenreich IV, 250:165. 1907.

Plants 10–45 cm. high, glabrate or but slightly lanate, especially around the heads; leaves ascending, 15–30 mm. long, the spinose lobes from 2–15, usually 6, twice to many times longer than the width of the rachis; flower clusters almost entirely terminal, frequently as much as 20-flowered; corolla deep blue, 15–19 mm. long; lobes 5–6 mm. long; stamens 3–4 mm. long. (Plantae 10–45 cm. altae, glabratae; capitulis leviter lanosis, terminalibus; foliis ascendentibus, 15–30 mm. longis; lobis spinosis, 2–15, saepissime 6, linearibus aut anguste lanceolatis, 3–12 mm. longis; lobis 5–6 mm. longis; staminibus 3–4 mm. longis.)

Type, from dry slope near Nellie, Palomar Mts., San Diego Co., Calif., at 5000 ft. alt., *P. A. Munz* 8341, in 1924, Pomona College Herbarium No. 48,414. Ranging most commonly in the mountains, at altitudes of from 4000–8000 ft., from Los Angeles and San Bernardino Counties to Northern Lower California, being most representative in the southern part of its range. Representative material studied, LOWER CALIFORNIA: Tanqui Canyon, *Jones* in 1928 (P). CALIFORNIA: San Diego Co., Laguna, *Cleveland* in 1885 (C); Palomar Mts., *Spencer* (P); Palomar Mt., *Chandler* 5372 (C), *Jones* in 1926 (P). Riverside Co., Tahquitz ridge, San Jacinto Mts., *Spencer* in 1923 (P); Idyllwild, San Jacinto Mts., *Jones* in 1924 (P), *Hall* 2384 (P); Strawberry Valley, San Jacinto Mts., *Grant* in 1901 (C); Hemet to Mt. San Jacinto, *J. T. Howell*, 574 (S.A.); 6 mi. southeast of Poppet Flat, *Munz* and *Johnston* 8837 (P). San Bernardino Co., Barton Flats, San Bernardino Mts., *Munz* and *Johnston* 9658 (P); Clark's, San

Bernardino Mts., *Jones* in 1900 (P); Green Valley, San Bernardino Mts., *Abrams* 2061 (P); Cactus Flats, San Bernardino Mts., *J. T. Howell* 334 (S.A.), *Johnston* in 1924 (P); Foresee Creek, San Bernardino Mts., *Grinnell* 42 (C); Seven Oaks, San Bernardino Mts., *Parish* 3685 (C), *Hall* 956 (P); Trail East of Hook's Hill, San Bernardino Mts., *Wilder* 317 (P); Coldwater, fork Lytle Creek, San Antonio Mts., *Johnston* 1385 (C, P), Coldwater Canyon, San Antonio Mts., 2682 (P, C); San Antonio Canyon; *Johnston* 1587 (C, P); Head of South Fork of Lytle Creek, San Antonio Mts., *Johnston* 1459 (P).

The following collections are atypical approaching var. *elongata*. CALIFORNIA: Los Angeles Co., Mt. Wilson, San Gabriel Mts., *Grinnell* in 1917 (P). Ventura Co., Cuddy Valley, Mt. Pinos, *Epling* and *Dunn* in 1931 (P); Upper Lockwood Valley, Mt. Pinos region, *Dudley* and *Lamb*, 4677 (S). Santa Barbara Co., Casmalia, *Eastwood* 867, and 758 (C.A.). Monterey Co., Santa Lucia Mts., *Eastwood* in 1893 (C); Santa Lucia Mts., Chew's Ridge, *Rowntree* in 1929 (P).

Although this variety intergrades freely in the lower altitudes with var. *elongata*, a long series shows it distinct enough to warrant recognition. It differs from var. *elongata* in the following ways: it is less woolly, lower growing, less branched above; the heads are larger and there are fewer axillary heads; the leaves have on the average 2–4 more lobes.

1e. **Gilia densifolia** Benth. var. **mohavensis** Craig n. var.

Plants low (8–30 cm.) canescent-lanate, stems brittle, densely much branched, ascending; leaves ovate-lanceolate in outline, 1–5 cm. long, reflexed and rigid, with the 2–8 short spinose lobes rarely longer than the width of the rachis; heads numerous, from 25 in very small plants up to 200 in large ones; corolla pale blue or pale lavender sometimes almost white, 15 mm. long, the lobes less than half as wide as long and about half the length of the tube; stamens 4½–5 mm. long. (Humilis, 8–30 cm. alta, canescenti-lanosa; caulibus facile fractis, dense et multe ramosis, ascendentibus; foliis ovato-lanceolatis, 1–3 cm. longis, reflexis et rigidibus; lobis foliorum 2–8, brevibus, spinosis, 1–4 mm. longis; rhachidibus 2–3 mm. latis; capitulis numerosis, 25–200; corollis pallide coeruleis, 15 mm. longis; lobis corollarum 5 mm. longis, 2 mm. latis; staminibus 4½–5 mm. longis.)

Type, from sand dunes between Rosamond and Mohave, Kern Co., Calif., *T. Craig* 1360, June 7, 1928, Pomona College Herbarium No. 182,-123; isotypes, University of California 494,768, and Pomona 182,264. Ranging rather widely over the Mohave Desert and most abundant in Antelope Valley. Representative material studied, CALIFORNIA: Inyo Co., Independence, *Peirson* in 1917 (F.P.); Lone Pine, *Jones* in 1897 (P). Kern Co., Red Rock Canyon, *Howell* 3190 (C.A.), *Hart* in 1926 (C.A.);

Sand Hills south of Mohave, *Munz* 11,069 (P); Betwen Rosamond & Mohave, *Newsom* in 1933 (P). Los Angeles Co., Ten miles south of Muroc, *Munz* and *Craig* 12,929 (P); Lancaster, *Hart* in 1925 (C.A.); Palmdale, *Abrams* and *McGregor* 518 (S). San Bernardino Co., Sand Dunes, Granite Mts., So. of Kelso, *Newsom* and *Hilend* in 1930 (P); The Pipes near Morongo Valley, *Jaeger* and *Keck* 244 (P).

The following sheets are quite intermediate with var. *elongata* and are of interest in that they show the relationship of var. *mohavensis* to *G. densifolia* rather than to *G. eremica* which it somewhat resembles in its low stature. Cameron, *Jones* in 1900 (P); Grade above Hackberry Canyon 8 mi. from Caliente, *K. Brandegee* in 1910; Warner's Hot Springs, *Buttle* in 1913 (C.A.); Edge of San Gabriel Mts., 3 mi. So. of Vincent, *Craig* 2029 (P); Vincent, *Craig* 2031 (P).

Specimens of var. *mohavensis* from the Antelope Valley and Granite Mts., show extreme variation from any of the other varieties of *G. densifolia*, and single sheets from these areas, but for the perennial habit, could not be recognized as belonging to this species, being much shorter, very compactly branching, and generally much paler in color in stem, leaf and flower. The plant is very brittle. The leaves are different in shape as already noted, and are strongly and rigidly recurved.

2. GILIA VIRGATA (Benth.) Steud., nom. ed. 2, 1:684. 1840. *Hugelia virgata* Benth., Bot. Reg. 19: sub. t. 1622. 1833; *Navarretia virgata* (Benth.) Brand, Pflanzenreich IV, **250**:167. 1907.

Plant annual, 8–50 cm. high, virgate to much branched; leaves filiform and entire, or parted into 3 filiform lobes; flower clusters 3–20-flowered; flowers pale sapphire blue to deep ultramarine, 8–15 mm. long; the lobes about half the length of the tube or longer; anthers linear sagittate.

G. virgata is the most common of all the annual *Hugelias*. There are a number of geographical races of the species, as would be expected in a species of such a variable group and with such a varied life condition, for *G. virgata* is found in almost all life conditions throughout cismontane Central and Southern Calif. and is represented by one variety on the western Mohave Desert. In one form or another it occurs from sea level to altitudes of over 8000 ft. Of these races, I am recognizing four as distinct enough to warrant varietal recognition. Of course, much intergradation occurs between these varieties; there is also some evidence of intergradation of *virgata* with other species; such as *G. filifolia* var. *typica* with *G. virgata* var. *typica*, and of *G. eremica* with some of the varieties of *G. virgata* from the south eastern part of its range. *G. virgata* blooms from late May through August, of very rarely as late as December.

KEY TO VARIETIES

A. Flower heads 1–3-very rarely 4-flowered. Stamens commonly of slightly irregular length. Corolla usually less than 12 mm. long; the lobes usually as long as tube.

B. Calyx always lanate. Bracts 2–5-lobed, 3-flowered heads common, corolla usually less than 10 mm. long.

2d. *G. virgata* var. *ambigua.*

BB. Calyx rarely at all lanate, sometimes thinly so, frequently glandular, bracts 1–3-lobed, 3-flowered heads rare, corolla 10–12 mm. long.

2c. *G. virgata* var. *sapphirina.*

AA. Flower heads 3–20-flowered. Stamens equal or very nearly equal in length. Corolla usually more than 12 mm. long; the lobes usually shorter than the tube.

B. Stem virgate commonly simple or with few branched (1–6) flower clusters; lobes of the corolla more than one third as wide as long. Coastal Central Calif.

2a. *G. virgata* var. *typica.*

BB. Stem always branching; flower clusters 5–100; corolla lobes less than one third as wide as long. Cismontane So. Calif.

2b. *G. virgata* var. *dasyantha.*

2a. **Gilia virgata** (Benth.) Steud var. **typica** n. nom. *Hugelia virgata* Benth., Bot. Reg. 19: sub. t. 1622. 1833; *Navarretia virgata* (Benth.) Brand, Pflanzenreich IV, **259**:165. 1907; *Navarretia densifolia var. lanata* Brand. l.c.

Plant white floccose, glabrate with age; stem usually simple and virgate 8–50 cm. high, or rarely branched from base and paniculately branched above; leaves slender, 15–50 mm. long, ascending often appressed to stem, entire, filiform, or more rarely parted into 3 linear lobes; flower clusters commonly terminal, or more rarely axillary, 3–20-flowered, surrounded by tripartate bracts 15–20 mm. long; calyx 8 mm. long; flowers regular blue 15 mm. long; the lobes 6 mm. long, more than one third as wide, stamens 5 mm. long, attached 1–2 mm. below sinuses; anthers 2 mm. long linear-sagittate.

Type locality, California, Douglas; probably near Monterey. Range, *G. virgata* var. *typica* is found in Coastal Monterey Co. Toward the south it merges with var. *dasyantha.* These intergrades can be found as far south as Ventura Co. Representative material studied, CALIFORNIA: Monterey Co., California, *Douglas* (C); Tularcetes, *Dudley* in 1901 (S); Carmel Valley, *McGregor* 93 (S); near Monterey, *Brewer,* in 1861 (C); Pajaro Hills, *Chandler* 454 (C); Seaside, Del Monte, *Heller* in 1903 (P); Seaside, Monterey, *Eastwood* 164 (C.A.); Carmel River, *Dudley* in 1905 (S); Palomar Creek & Arroyo Seco, Santa Lucia Mts., (S).

The following specimens are slightly atypical and approach variety *dasyantha* in being less lanate and somewhat more branched. San Benito Co., Pinnacles National Monument, *Craig* 1370 (P), *Sutliffe* in 1920 (C.A.). Ventura Co., Matilija Canyon, *Hoffmann* (S.B.).

Instead of being a widespread and abundant form as it is commonly regarded, *G. virgata* var. *typica* is a very localized race from Monterey Co., and is not common.

2b. **Gilia virgata** var. **dasyantha** (Brand) n. comb. *Navarretia virgata* var. *dasyantha* Brand, Pflanzenreich IV, **250**:168. 1907; *Hugelia virgata* var. *dasyantha* (Brand) Jepson, Man. Fl. Pls. Calif., 793, 1925.

Plant 5–35 cm. high, white floccose, glabrate in age, usually much branched both from base and nodes, leaves linear or divided into 3 linear lobes ascending or reflexed, flower clusters from 5–over a hundred, 3–10-flowered; bracts usually 6–14, commonly 8 mm. long; flowers regular or very slightly irregular, blue 14 mm. long; lobes almost 6½ mm. long less than one third as broad; stamens yellowish, 5 mm. long, attached about 1 mm. from sinuses; anthers 1½ mm. long, linear-sagittate.

Type, I have been unable to ascertain the type of this variety. Brand cites Hall 98 as the type, but I have been unable to locate this collection, unless the Hall collection from Riverside, July 3, 1897 (C) is this collection. San Bernardino, *Parish*, 1478 (C); *Parish* 3803 (C); So. Calif., *Parry* and *Lemmon* 249 (P) are all cited by Brand as "typical" *dasyantha*. These show beyond reasonable doubt to which plants *dasyantha* should refer. Ranging throughout cismontane Southern California south of Santa Barbara County. Representative material studied, CALIFORNIA: San Diego Co., San Onofre Canyon, *Hitchcock* in 1929 (P). Orange Co., Trabuco Canyon, *Abrams* 1791 (P); Rancho Santa Ana, *J. T. Howell* 73 (S.A.). Riverside Co., Wilder's near Riverside, *Wilder* 45 (C); Temecula, *Jones* 1926 (P); Riverside, *Hall* in 1897 (C). Ventura Co., Santa Susanna Pass, *J. T. Howell* 1020 (S.A.). Santa Barbara Co., Hot Springs, *Dudley* in 1896 (S). Los Angeles Co., Santa Monica Mts., *J. Ewan* 3480 (P); Downey, *Zumbro* 58 (P); San Fernando Valley, *Barber* 168 (P, C); Los Alisos Canyon, *Epling* and *Dunn*, in 1931 (C); Pomona, *Chandler* in 1897 (C); Sierra Madre, *Abrams* 2636 (P). San Bernardino Co., Plains near San Bernardino, *Parish* 11,888 (C); Colton, *Braunton*, 475 (C), *Pringle* in 1882 (P); San Bernardino, *Parish* in 1900 (P); Dry Mesas, San Bernardino Valley, *Parish* 11,376 (C), albino plant; Near Bloomington, *Parish* 11,-282 (C), Cucamonga, *Abrams* 2661 (P); Claremont, *Craig* 1860 (P), *Munz* 2240 (P), *Baker* 3345 (C, P), *W. R. Shaw* in 1900, albino plant, *Craig* 529 (P), dated Nov. 24, 1927—blooming into the second season, *Munz*, 4404 (P), dated Dec. 5, 1920—growing into the second season.

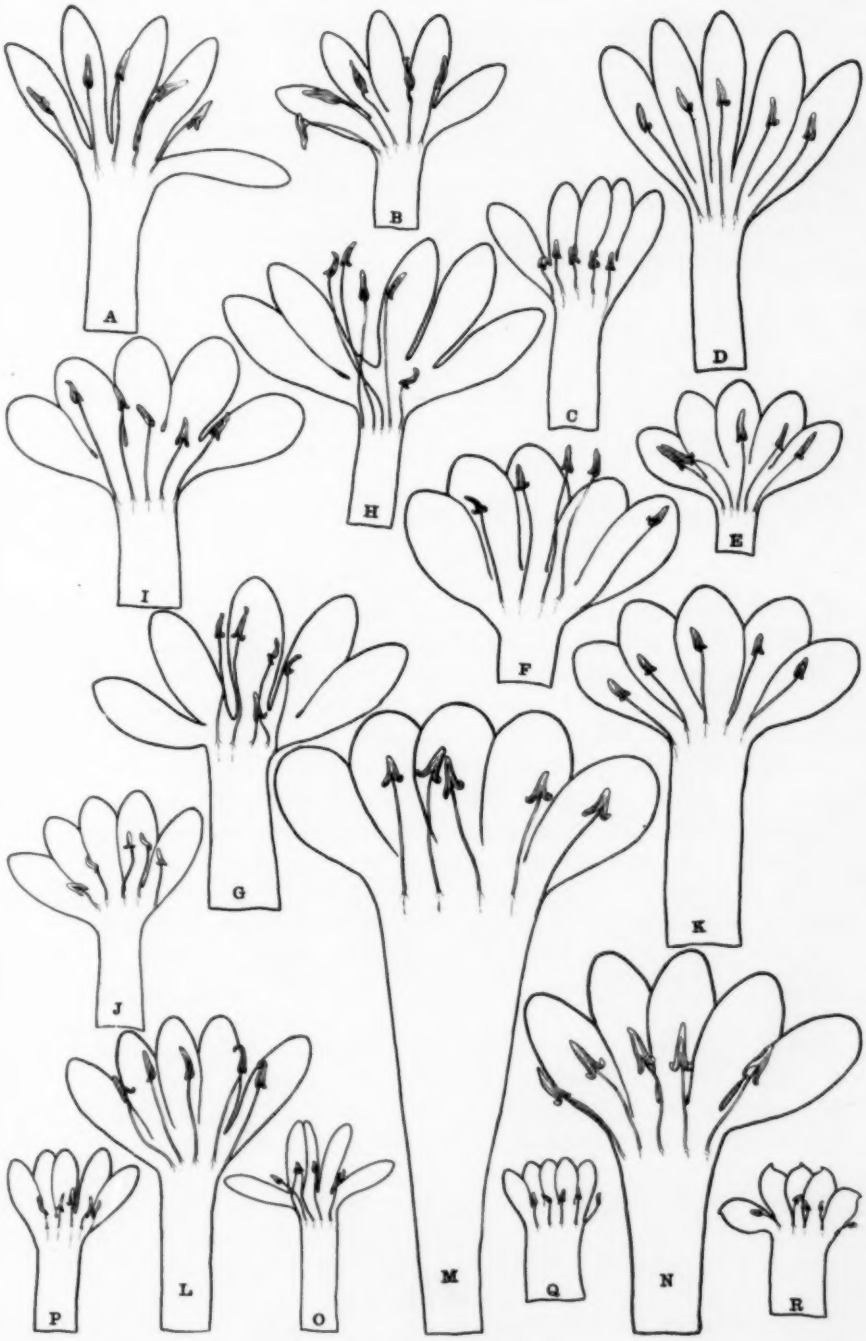
Var. *dasyantha* is the commonest variety of *G. virgata*. It differs from var. *typica* in being much more branched, slightly smaller, more slender flowered, in having smaller but more numerous flower clusters. It is highly variable and intergrades to some extent with all the other varieties of the species.

The following collections represent a race of var. *dasyantha* differing from typical form in the coarseness of its growth. Riverside Co., Cabazon, *Munz* 898 (P). San Bernardino Co., Mentone, *R. F. Smith* 81 (C).

(To be concluded)

Explanation of plate 23

Fig. A. *G. pluriflora*—Lemon Cove, Tulare Co., Cal., *Condit* in May (P.) Fig. B. *G. lutescens*—Santa Ana Mts., Cal., *Munz* 7103 (P.) Fig. C. *G. Wilcoxxi*—10 mi. n. e. of Reno, Nev., *Munz* 11,100 (P.) Fig. D. *G. virgata var. dasyantha*—San Bernardino Valley, Cal., *Parish* 11,281 (P.) Fig. E. *G. virgata var. ambigua*—Wrightwood, San Gabriel Mts., Cal., *Munz* and *Johnston* 11,197 (P.) Fig. F. *G. virgata var. sapphirina*—North base of Sugar Loaf Mt., San Bernardino Co., Cal., *Munz* 10,760 (P.) Fig. G. *G. eremica var. typica*—2½ mi. east of Barstow, Cal., *Woolf* 5390 (S.A.) Fig. H. *G. eremica var. zionis*—Zion National Park, Utah, *Craig* 1418 (P.) Fig. I. *G. eremica var. arizonica*—Wickenburg, Ariz., *Jones* in 1903 (P.) Fig. J. *G. eramica var. Yageri*—Yagers north of Tucson, Ariz., *Jones* in 1890 (P.) Fig. K. *G. Sherman-hoytae*—12 mi. so. of Muroc, Cal., *Peirson* 7268 (P.) Fig. L. *G. densifolia var. mohavensis*—between Rosamond and Mohave, Kern Co., Cal., *Craig* 1360 (P.) Fig. M. *G. densifolia var. sanctora*—Santa Ana River Wash, Cal., *Reed* 3107 (P.) Fig. N. *G. densifolia var. austromontana*—San Jacinto Mts. Cal., *Munz* and *Johnston* 8837 (P.) Fig. O. *G. filifolia var. typica*—San Diego, Cal., *Brandegee* in 1906 (C.) Fig. P. *G. filifolia var. sparsiflora*—Cactus Flats, San Bernardino Co., Cal., *Munz* 10,500 (P.) Fig. Q. *G. filifolia var. diffusa*—Colorado Desert, Calif., *Munz* 11,921 (P.) Fig. R. *G. filifolia var. Harwoodii*—So. of Rice, Riverside Co., Cal., *Wolf* 3119 (S.A.).



CRAIG: HUGELIA

INDEX TO AMERICAN BOTANICAL LITERATURE
1930–1934

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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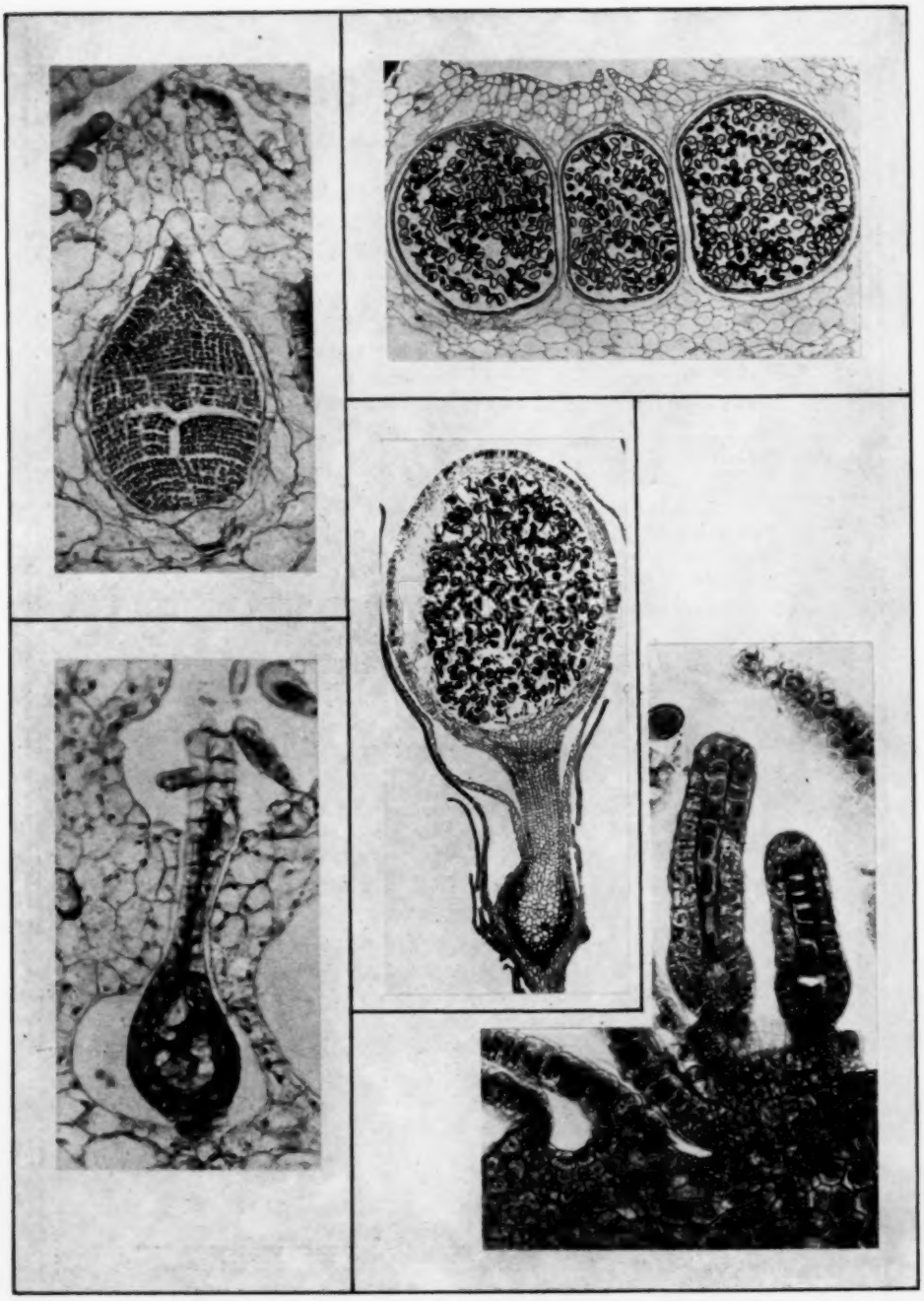

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